REPRODUCTIVE CYCLE OF THE DUNGENESS CRAB,

CANCER MAGISTER, IN SOUTHEASTERN ALASKA

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A

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Abstract

This study examined if female Dungeness crabs in Alaska reproduce annually. Crabs (287) were reared in flow-through tanks for one year and gonadosomatic indexes (GSI) and oocyte areas were calculated for seven months. Non-reproducing females had higher GSI and oocyte areas than reproducing females ($P<0.0001$); resorption of gonads was observed. Male GSI varied significantly over the year. Crabs (27,506) were sampled with commercial pots and scuba in April and September in Glacier Bay, Alaska from 1992 to 1998. A large percentage (86%) of nonovigerous females were observed in the spring when females should be brooding eggs. Molting probability is reduced as females become larger and they rely on stored sperm to fertilize eggs. A tagging study confirmed some females skip at least one mating season and extrude eggs in another season without ecdysis. This study demonstrated not all mature female Dungeness crabs in Alaska, especially larger females, reproduce annually.

Table of Contents

List of Figures

List of Tables

List of Appendices

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CHAPTER 1: REPRODUCTION OF MALE AND FEMALE DUNGENESS CRABS, *CANCER MAGISTER*, IN SOUTHESTERN ALASKA

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Abstract

Dungeness crabs are believed to reproduce annually, but may not in Alaska, the northern limit of their range. The objectives of this study were to: determine if there is seasonal variation in gonadal development of male Dungeness crabs in Alaska, compare gonadal development in ovigerous and nonovigerous females Dungeness crabs in Alaska, and determine if female Dungeness crabs in Alaska reproduce annually. Crabs from southeastern Alaska were reared in flow-through tanks from October 1997 through October 1998. All crabs were tagged and assigned to groups based upon gender and reproductive status: 1) non-ovigerous females at the time of collection (and that did not extrude eggs in the following months) were denoted as non-reproductive (NR) in 1997; 2) ovigerous females were incubating eggs and therefore reproduced (R) in 1997; and, 3) male crabs (M). Changes in gonad development were followed over a reproductive cycle for R, NR and M crabs. Gonadosomatic indexes (GSI) and oocyte areas were calculated monthly from March through October 1998. GSI and oocyte areas were used to compare gonad development between R and NR females. Male GSI increased significantly over time. NR females had significantly higher GSI and oocyte areas than R females. October GSI decreased significantly from September GSI among NR females in the laboratory and field, suggesting resorption of gonads. All mature females do not reproduce annually in southeastern Alaska. Under laboratory conditions, some females reproduce in consecutive years. The reproductive cycle of Dungeness crabs appears to be complex and warrants additional study.

Introduction

Dungeness crabs, *Cancer magister*, are distributed from the Pribilof Islands, Alaska to Santa Barbara, California (Jensen, 1995). They inhabit bays, estuaries and the open ocean near the coast (Hoopes, 1973) and range from the intertidal (Hart, 1982) to 200 meters depth (T. Shirley, unpublished data). Dungeness crabs most commonly inhabit sandy or muddy sand areas, but can be found on almost any substrate (MacKay,1943; Cleaver, 1949; Hipkins, 1957; Hoopes, 1973). They are generally thought to be opportunistic carnivores and scavengers (Hoopes, 1973), but there may be some prey selectivity. Stevens *et al.*(1982) found that fish and shrimp *Crangon* spp. appear to be the most important prey of Dungeness crabs in a Washington estuary. *Cancer magister* undergo ontogenetic changes in feeding patterns (Stevens *et al.*, 1982) and juveniles have been found to be omnivorous, not strictly carnivorous as was previously thought (Jensen and Asplen, 1998).

Dungeness crabs support important commercial fisheries from central California to Kodiak, Alaska and are the oldest known shellfish fishery of the north Pacific Coast (Hipkins, 1957). Only male Dungeness crabs greater than 165 mm in carapace width may be retained in the crab fisheries of Alaska within predetermined seasons (Alaska Department of Fish and Game, 1998). Southeastern Alaska and Yakutat contributed 47% of the cumulative catch of Dungeness crabs in Alaska between 1969-1994 (Orensanz *et al.*, 1998). In recent years, southeastern Alaska has become a larger contributor to the landings in Alaska due to reduced landings in the other Alaskan fishing areas. From 1992-1997 southeastern Alaska contributed 64% of the cumulative Alaskan Dungeness

harvest and for both 1996 and 1997 southeastern Alaska contributed 81% of the total Alaska catch. In 1997 the ex-vessel value of the Dungeness fishery in Alaska was $11,098,114 (personal communication S. Shirley, State of Alaska Commercial Entry Fisheries Commission).

Throughout most of southeastern Alaska, commercial fishing for Dungeness crabs is limited to June 15 through August 15 and October 1 through November 30 (Alaska Department of Fish and Game, 1998). These fishing seasons were set to avoid sensitive periods in Dungeness crab reproductive cycles. *Cancer magister* in southeastern Alaska begin mating and extrude eggs from September through November (Shirley *et al.*, 1987). Male Dungeness crabs molt prior to mating and are susceptible to damage when in a soft-shelled state, therefore, commercial fishing is not allowed August 16 through September 30. Eggs hatch April through August with most of the hatching occurring in May and June (Shirley *et al.*, 1987). Dungeness crabs have a prezoea, five zoeal, and a megalopa stage (Shirley *et al.*, 1987). In southeastern Alaska, the megalopa stage begins settling out of the water column August and September and may continue settling thereafter (Shirley *et al.*, 1987).

Cancer magister sexes are dimorphic and mating occurs between hard-shelled males and soft-shelled females (MacKay, 1943; Butler, 1960; Snow and Neilsen ,1966; Hoopes, 1973). After copulation, sperm is stored in paired spermathecae and eggs are fertilized as they pass by the spermathecae during extrusion (Jensen *et al.*, 1996). The eggs form a spongelike mass, adhering to the setae on the pleopods and are brooded until hatching (Wild, 1980; Jaffe *et al.*, 1987).

Crustaceans generally fall into one of two reproductive strategies. Asynchronous breeding within a specific time of the year is common in crustaceans from temperate, subtropical and tropical regions. Females in these populations are usually out of phase, but the population as a whole begins and stops breeding at the same time. Asynchronicity can result from the production of several clutches by the females or by production of a singe clutch by each female out of phase. In a synchronously breeding population all females are ovigerous at the same time and breeding is usually restricted to a short period; at any time of the year all ovaries or eggs will be in about the same stage of development (Sastry, 1983). Generally, crustaceans with planktotrophic larvae linked with peak primary production breed synchronously in higher latitudes and asynchronously or continuously in lower latitudes where primary production is not pulsed (Sastry, 1983).

Vitellogenesis among crustaceans occurs in two stages. In primary vitellogenesis, yolk is deposited slowly and oocytes increase gradually in size. During secondary vitellogenesis, large amounts of yolk are deposited relatively quickly and oocytes increase synchronously and more rapidly to their mature size (Adiyodi, 1985; Charniaux-Cotton, 1985; Nelson 1991; Talbot and Helluy, 1995). Secondary vitellogenesis may occur only during the reproductive season among crustaceans (Charniaux-Cotton, 1985).

Water temperature, diet, photoperiod and other environmental conditions have been linked to the timing of mating and egg production in many crustaceans including the spiny lobster, *Panulirus argus* (Kanciruk, 1980) and the American lobster, *Homarus americanus* (Waddy and Aiken, 1991). Water temperature influences size at maturity,

time of spawning, coordination of molting and spawning cycles, time of hatching, and success of egg attachment and incubation in the American lobster (Waddy and Aiken, 1991). Variations in the reproductive cycle of lobsters are common at the northern and southern ends of their range where water temperatures are not optimal (Waddy *et al.*, 1995). In general, species inhabiting cold waters (<10°C) have much longer embryogenic periods than those living in warmer water because low water temperatures decrease the rate of embryogenesis (Shirley *et al.*, 1987; Shields, 1991).

Dungeness crabs are generally thought to extrude eggs annually (Wild, 1983a; Jaffe *et al.*, 1987), but this may not be true for Dungeness crabs in southeastern Alaska. Alaska is the northern limit of the range for Dungeness crabs, and this may affect the periodicity of reproduction. Different populations of the same species may vary in duration and frequency of reproductive cycles in different areas of their range, especially those occurring at higher latitudes (Sastry, 1983).

The only study to date in which ovary development was examined in Dungeness crabs compared crabs in central and northern California. Ovaries from the two areas developed at similar rates. The crabs from northern California produced more ovarian tissue than the crabs from central California (Wild, 1983a). Crab ovaries began redeveloping soon after egg extrusion, while the crabs were brooding their eggs (Wild, 1983a).

Gamete production requires energy and an organism must allocate energy to this process (Sastry, 1983). Ovigerous female Dungeness crabs have significantly lower feeding rates and foraging responses than nonovigerous females (Schultz and Shirley,

1997). Likewise, ovigerous *Cancer pagurus* in the laboratory have been found to have reduced metabolic rates (Naylor *et al.*, 1997). Some ovigerous crabs, such as Dungeness crabs in Alaska, may not have energy to allocate to gonad production until after their eggs hatch. Conversely, the spider crab, *Maja squinado*, are able to extrude eggs a few days after the previous brood hatches. Therefore, maturation of the ovaries is simultaneous with the development of eggs (Gonzalez-Gurriaran *et al.*, 1993). Similarly, the brachyuran crab, *Metopograpsus messor*, undergoes another vitellogenic cycle immediately following egg extrusion so gonads are developing while the female is brooding eggs (Sudha and Anikumar, 1996).

Reproductive cycles have not been examined for the males of many crustacean species. Where it has been examined, seasonal changes have been found in some species such as the Japanese mitten crab (Kobayashi and Matsuura, 1995) and *Gaetice depressus* (Fukui, 1993). In other populations examined there appeared to be continuous activity throughout the year (Sastry, 1983). No study has examined seasonal changes of gonads in male Dungeness crabs.

Efficient management of crab fisheries requires knowledge of the reproduction and life history of the exploited species. It is surprising how little is known about the reproductive biology and ecology of these organisms (Shields, 1991). Gonadosomatic indexes (GSI) are the simplest indicator of reproductive state (Grant and Tyler, 1983a). GSI are useful in examining changes in ovary size over time, but are not a good predictor of developmental stage (West, 1990). Ovarian maturation is a complex process and should not be described by just one parameter (Grant and Tyler,1983a; West, 1990).

Some argue that oocyte measurements are the best method for examining reproductive cycles in invertebrates, in part because oocyte measurement data are independent of the size of organisms (Grant and Tyler, 1983b). A combination of gonadosomatic indexes and oocyte measurements can yield a more complete picture of reproductive cycles.

Most gonad development studies have captured animals from the field and immediately dissected them. The reproductive history of crabs from the field is unknown and it is not possible to track development between different groups. This study was unique because crabs were separated and individually tagged at the beginning of the study into three groups: males, females that reproduced in 1997 and females that did not reproduce in 1997. All groups of crabs were monitored in the laboratory for a year. Gonad development was then analyzed for each group and compared.

Gonadosomatic indexes and oocyte measurements were used to examine reproductive cycles of Dungeness crabs in southeastern Alaska. The three objectives of this study were to: determine if there is seasonal variation in gonadal development of male Dungeness crabs in Alaska, compare gonadal development in ovigerous and nonovigerous female Dungeness crabs, and determine if female Dungeness crabs in Alaska reproduce annually.

Methods and Materials

Female Dungeness crabs were collected from Bridget Cove near Juneau, Alaska October 1997 to October 1998 (Figure 1). Females were collected by SCUBA, commercial Dungeness crab pots and wading at night during spring low tides with flashlights and dip-nets (Appendix 1). Male crabs were collected from Glacier Bay

National Park and Preserve in October 1997 using commercial Dungeness crab pots (Figure 1, Appendix 1). All crabs collected were measured with vernier calipers to the nearest millimeter immediately anterior to the tenth anterolateral spine; sex and reproductive state were recorded and a numbered tag was attached to each crab.

Only crabs that were assumed to be mature were used in this study. A histological study suggested that male Dungeness crabs are sexually mature at 108[1] mm carapace width (CW), but the smallest male they observed in a pre-mating embrace was 131[1] mm CW (Butler, 1960). A mature female for this study was defined as one that could produce a viable egg clutch, not simply a female large enough to mate. In general, females Dungeness crabs are considered mature at approximately 93[1] mm CW (Butler, 1960; Orensanz and Gallucci, 1988). A long term study in Glacier Bay National Park and Preserve has suggested that females in the area are mature at approximately 100 mm CW and females 106 mm were found with egg clutches (Swiney, 1999). All females in this study were 106 mm CW or larger.

The Dungeness crabs were held in flow-through tanks at the Juneau Center, School of Fisheries and Ocean Sciences wet lab, and the National Marine Fisheries Service, Auke Bay Laboratory. The tanks had flowing seawater from 30m depth in Auke Bay. Crabs were fed *ad libitum* a diet of fish and squid biweekly. Water temperature and salinity were recorded weekly (Appendix 2). Crabs were dissected monthly for

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[1]Carapace widths have been converted because early researchers initially measured crabs including the 10th anterolateral spine and for this study all crabs were measured excluding this spine. The equation used in the conversion was Y=0.0715X-0.029 where Y= the combined length of the 10th anterolateral spine and x= carapace width exclusive of the spines (Butler, 1961).

gonadosomatic index calculations and oocyte area measurements.

Females held in the laboratory were assigned to one of two groups based on their reproductive status when initially collected. Nonovigerous females at the time of collection (and that did not extrude eggs in the following months) were denoted as females that did not reproduce in 1997. Female crabs that extruded eggs in 1997, were considered to have reproduced in 1997. With this distinction among females it was possible to compare the changes in gonad development over a reproductive cycle with crabs that reproduced (extruded eggs) in 1997 and those that did not.

Crabs were held in tanks for one full year, and reproductive state was recorded for all, including date of egg extrusion if applicable. Crabs were dissected March 1998 through October 1998. To dissect the crabs the carapace was first removed. The gonads, ovaries in the females and vas deferens and testis in the males, were then dissected. The gonads and body were dried at 60° C to constant weight. A small amount of the ovaries from each female and eggs if present, were preserved in Stockard's solution. Microscope slides of gonads were made by placing a small amount of gonad and one drop of glycerin on a microscope slide. To prevent the gonads from being damaged when the cover slip was placed on the slide, a small piece of clay was put on each corner of the cover slip. An image analysis program (Optimas, 1993), a compound microscope equipped with a video camera, and a computer were utilized to digitally capture gonad images from the microscope slide. Gonad and egg color was quantified by using paint color charts. Ovary color has been tested statistically as an index of ovary maturity and has been found to be useful (Wild 1983a).

Gonadosomatic Index

A sample size of 10 crabs was achieved or exceeded every month for all males and females that did not reproduce in 1997, with the exception that only 7 females were sacrificed in April. Unfortunately, a sample size of 10 was achieved only in 3 months for females that reproduced in 1997. No crabs were sacrificed from this group in August in order to have crabs for the remainder of the study. Two crabs died in September and were immediately dissected. In April, July and October, five females that reproduced in 1997 were dissected.

Gonadosomatic indexes (GSI) were calculated by the equation (Appendix 3):

$$GSI = \frac{gw}{bw} * 100$$

gw=gonad weight
bw=body weight

If a crab was missing an appendage, the same appendage from the other side was dried separately and added twice into the total body weight calculation.

As a control for laboratory effects, additional crabs from Bridget Cove were collected periodically (Figure 1, Appendix 1). Eight males were sacrificed in September and 10 in October. Nonovigerous female crabs from the field were sacrificed as follows: 3 in April, 10 in July, 9 in September and 10 in October. Five ovigerous females were sacrificed in April and 3 were sacrificed in October. It was not possible to determine the recent reproductive history of these females, therefore, they could not be categorized into groups based upon reproductive activity in 1997. Comparisons could only be made based upon the current reproductive state of these females. The same laboratory methods

were used for these crabs as for the crabs reared in the laboratory, including GSI calculation.

Oocyte Measurements

The area of twenty oocytes per female crab dissected were measured using the image analysis program (Optimus, 1993, Appendix 3). Area was used rather than size or diameter to eliminate possible measurement bias due to imperfect sphericity of oocytes. Preserved oocytes were not used in this study because gonads were immediately digitized upon removal from the crab. Preserving cells can introduce a bias because the preserving agent can change the size and shape. Oocyte areas were not measured for crabs that extruded eggs in the laboratory, which were considered "spent" (Grant and Tyler, 1983b). During the spent stage there are few measurable oocytes. If measured, only these few larger oocytes would be used to represent the entire oocyte mass, and the oocyte area estimates would have been highly elevated and inaccurate.

Statistical Analysis

Analyses of variance (ANOVA) of GSI and oocyte area were calculated for all treatments to determine if GSI and oocyte area varied over time (StatView, 1996). Scheffé's F test for post-hoc comparisons was used to determine within a group which months were statistically different from each other if the ANOVA was significant (StatView, 1996). Means, variances and standard errors were calculated each month for the three groups. Mean gonadosomatic indexes, oocyte areas and average water temperatures in tanks were plotted by month for all treatments. Paired *t*-tests were used

to determine if there were significant differences between field and laboratory data for each month that field data were available (StatView, 1996).

Female data were further evaluated by comparing the GSI of crabs that did and did not reproduce in 1997. The mean carapace width (CW) for both groups were calculated and a paired *t*-test was implemented to determine if there was a significant difference between the CW in each group (StatView, 1996). To determine if a significant difference occurred between the two groups of data, a general linear model, similar to a 2 factor ANOVA, was used (SYSTAT, 1998). Because there was no reason to expect a similar trend in GSI for the two types of females, a main effect of crabs that reproduced and those that did not reproduce was not included in the model. Thus, the model contained an effect of month and tested for differences between females that reproduced and did not reproduce in 1997 through the interaction term for month and group.

The Pearson correlation coefficient was used to determine if there was a relationship between oocyte area and GSI (StatView, 1996). Laboratory data were pooled and examined separately for females that reproduced and those that did not.

Statistical methods, as described by Sokal and Rohlf (1995), were used in calculations. Error bars represent one standard error of the mean. Values were considered significant when $P<0.05$ and highly significant when $P<0.01$.

Results

A total of 287 crabs were sacrificed between March 1998 and October 1998. Eighty-two males, 97 females that did not reproduce in 1997 and 50 females that reproduced in 1997 were sacrificed from the laboratory. In addition, 18 males, 32

nonovigerous females and 8 ovigerous crabs were collected from the field and sacrificed. All crabs used in this study were assumed mature. Male carapace width ranged from 142 mm to 198 mm, female carapace width for crabs that did not reproduce in 1997 ranged from 106 mm to 170 mm, and female carapace width of females that did reproduce was 119 mm to 166 mm. There was no significant difference between the carapace widths of the two groups of females (*t*-test, t=0.3, P<0.05).

Gonadosomatic Index Temporal Variation

MALES

Temporal Trends

Male GSI varied highly significantly over time (ANOVA F=2.7, P=0.01). GSI generally increased March through June, reached a maximum in July and slowly decreased thereafter (Figure 2). There were no significant differences in GSI between individual months (Scheffé's F, P>0.05).

Field and Laboratory Comparisons

The mean GSI of males from the field were lower than the laboratory GSI in September and October, however only the October GSI were significantly different (*t*-test, t=2.1, P<0.05, Figure 2, Table 1).

NON-REPRODUCTIVE FEMALES

Temporal Trends

Laboratory females that did not reproduce in 1997 had a highly significant increase in GSI through the duration of this study (ANOVA F=11.5, P<0.0001). At the end of May water temperature began to increase sharply (Appendix 2), the eggs hatched

in females that reproduced in 1997, and at this time there was an increase in GSI of non-reproducing females that continued through September (Figure 3). October GSI decreased significantly from September (Scheffé's F, P=0.0006; Figure 3) which suggests resorption of gonads since these females did not extrude eggs. Resorption of gonads was also observed in females from the field (*t*-test, t=2.2, P<0.05; Figure 4). The GSI of laboratory females in both August and September were significantly different than March, April, May and June (only September) (Scheffé's F, P>0.045). There were also significant differences in August and September GSI in comparison to October GSI (Scheffé's F, P>0.013).

In total, 19 females that did not reproduce in 1997 extruded eggs in 1998 (Appendix 4). Five females extruded eggs at the end of August and the remaining 14 females extruded eggs throughout the month of September. The GSI of these females that extruded eggs were recorded in September and October (Figure 3, Appendix 3). In the month of August 10% (5 of 50) of the females extruded eggs, in September 48% (19 of 40) of the remaining females were ovigerous and in October 47% (9 of 19) of the remaining females were ovigerous. At the end of the study, a little less than half of the laboratory females that did not extrude eggs the previous year extruded eggs. It is not known if the females that were dissected throughout the study would have extruded eggs or not.

Field and Laboratory Comparisons

GSI of field nonovigerous females was significantly higher in the month of April than nonovigerous females from the laboratory (*t*-test, t=-2.4, P<0.05, Table 1).

Alternately, in July, the GSI of nonovigerous females from the field were highly significantly lower than nonovigerous laboratory females for the same month (*t*-test, t=3.0, P<0.01, Table 1). In both September and October, nonovigerous females from the field had lower GSI than nonovigerous laboratory females, but no significant differences were detected in either month (Figure 4, Table 1). GSI decreased significantly in September to October among nonovigerous field crabs (Scheffé's F, P=.03, Figure 4). The recent reproductive history of the females from the field was not known and probably represent both females that reproduced in 1997 and those that did not. Therefore, a comparison of field and laboratory females is not completely valid.

REPRODUCTIVE FEMALES

Temporal Trends

Laboratory females that reproduced in 1997 had a highly significant increase in gonad mass through the duration of this study (ANOVA F=53.7, P=<0.0001, Figure 3). The eggs of these females hatched and water temperature increased at the end of May (Appendix 4). Beginning in May, there was an increase in GSI that continued through October for reproducing females (Figure 3). The GSI in March, April, May, June, and July in this group were significantly different from GSI in September and October (Scheffé's F, P<0.02). GSI in September and October were also significantly different from each other (Scheffé's F, P=0.02). In the last month of the study 38% (3 of 8) of the remaining females extruded eggs (Appendix 4). These three females that reproduced in 1997 and extruded eggs in 1998 extruded eggs at the end of September and their GSI were calculated in October (Figure 3).

Field and Laboratory Comparisons

There were no significant differences between field and laboratory ovigerous female GSI for the months of April and October (*t*-test, April t=0.8, P>0.05; October t=-0.7, P>0.05, Table 1).

Comparison of Reproductive and Non-Reproductive Females

The temporal GSI of females that did not reproduce in 1997 was higher than the GSI of females that did reproduce in 1997 (Figure 3). A general linear model, which was a modified 2 factor ANOVA, was highly significant in both the month effect (F=20.0, P<0.0009) and the interaction effect of month and if the crab reproduced or not (F=8.2, P<0.0009).

In the last month of this study, 47% of the remaining females that did not reproduce in 1997 extruded eggs in 1998 and 38% of the remaining females extruded eggs in both 1997 and 1998.

Oocyte Area Temporal Variation

NON-REPRODUCTIVE FEMALES

Temporal Trends

The size of the average oocyte area increased over time in laboratory females that did not reproduce in 1997 (ANOVA, F=17.4, P<0.0001, Figure 5). Mean oocyte areas in March and April differed from oocyte areas in June (March only), July, August, September and October (Scheffé's F, P>0.027). Lastly, mean oocyte area in May differed from September and October (Scheffé's F, P>0.006).

Field and Laboratory Comparisons

Field data for nonovigerous females were available for 4 months. In the months of July (*t*-test, t=3.8, P<0.01, Table 1) and October (*t*-test, t=3.6, P<0.01, Table 1) mean oocyte areas of laboratory reared nonovigerous females were higher than field nonovigerous females. No significant differences were detected between oocyte areas of nonovigerous females in either April or September.

REPRODUCTIVE FEMALES

Temporal Trends

Mean oocyte area of females from the laboratory that reproduced in 1997 increased highly significantly over time (ANOVA F=14.6, P<0.0001, Figure 5). After May, when water temperature had increased (Appendix 2), and hatching had occurred, there was a large and constant increase in oocyte area for females that reproduced in 1997. Oocyte area in both September and October differed from March, April and May (Scheffé's F, P>0.017). Oocyte areas differed between the months of March and July as well as June and October (Scheffé's F, P>0.02).

Field and Laboratory Comparisons

Field data for ovigerous females were only available for April and oocyte areas of ovigerous laboratory and field crabs did not differ significantly (*t*-test, t=0.02, P>0.05, Table 1). Ovigerous females were collected from the field in October, but oocyte measurements were not made on these crabs since they were assumed to have recently extruded eggs.

Comparison of Reproductive and Non-Reproductive Females

Mean oocyte area was lower among females that reproduced in 1997 in comparison to females that did not reproduce in 1997 (Figure 5). A general linear model, which was a modified 2 factor ANOVA, was highly significant with respect to month effect ($F=28.4$, $P<0.0009$) and had a significant interaction effect of month and whether the crab reproduced or not ($F=2.2$, $P=0.05$).

Gonadosomatic Index and Oocyte Measurement Comparisons

Trends in gonadosomatic index and mean oocyte measurements were similar for laboratory females that did not reproduce in 1997 (Figure 6). Oocyte area increased more constantly over time, whereas GSI was about the same from March to May and then began to increase thereafter. GSI decreased sharply in October for this group of females, but oocyte area continued to increase, although the increase was not significant (Figure 6).

GSI and oocyte area more closely tracked each other in laboratory females that did reproduce in 1997 (Figure 7). GSI and mean oocyte area for this group remained relatively constant March through May and then both GSI and mean oocyte area began to increase after May, the time of egg hatching.

A linear correlation between GSI and oocyte area is suggested for all females reared in the laboratory ($p=0.8$, Figure 8a), but October females that did not reproduce were outliers. In October, GSI of females that did not reproduce significantly decreased from September (Scheffé's F, $P=0.006$; Figure 3). Therefore, the outliers were October crabs with decreased GSI and increased oocyte area (Figure 8a). With the removal of

October females that did not reproduce, the correlation coefficient was higher, thus suggesting a better relationship between GSI and oocyte area (p=0.9, Figure 8b).

GSI and mean oocyte area for laboratory females that did not reproduce, excluding October data (Figure 9a), were also correlated (p=0.8). Likewise, the relationship between GSI and mean oocyte area of females that reproduced (Figure 9b) had a high correlation (p=0.9).

The scattergrams of GSI and oocyte area for all females have a group of points with high GSI values and low oocyte areas (Figure 8a, Figure 8b, Figure 9a). These are non-reproducing females from the months of March and April. Examination of mean GSI and oocyte area show the same results for these females; high GSI values compared to oocyte areas (Figure 6).

Discussion

Seasonal Patterns of Gonadal Development

Males

Seasonal gonad development of male crustaceans has not been widely studied. When examined, some male crustaceans seem to have seasonal spermatogenesis activity and others appear to have continuous activity throughout the year (Sastry, 1983). Dungeness crabs in southeastern Alaska are thought to mate primarily from September through December (Shirley *et al.*, 1987; Shirley and Shirley, 1988; Schultz and Shirley, 1997). GSI of laboratory reared male crabs increased throughout this (Figure 2). Although the changes in GSI were less than 0.15%, an almost doubling of gonad mass

was observed (Figure 2). Male Dungeness crabs in southeastern Alaska appear to undergo seasonal gonadal development with peak gonad mass observed in July.

Females

Mature female Dungeness crabs are believed to reproduce annually, but females in southeastern Alaska may not. In a prior study, female Dungeness crabs were held in tanks from September through May in southeastern Alaska and none of the nonovigerous females extruded eggs (Schultz and Shirley, 1997). My observations on collections and tagged crabs from Glacier Bay National Park and Preserve, Alaska also suggested that some females in the area do not reproduce annually (Swiney, 1999). If reproduction is synchronous and annual, then all mature females should be ovigerous during the brooding season (April samples), but this is not the case in Glacier Bay; a large number of the female population collected was nonovigerous during April samples (Swiney, 1999). Crustacean reproductive cycles can vary radically depending on where in the range the species is studied. The spiny lobster *Panulirus argus* has been reported as reproducing once or multiple times a year or to have continuous reproduction in different areas of its range (Kanciruk, 1980).

A highly significant difference was detected in gonad development of laboratory reared females that did and did not reproduce in 1997. Females that reproduced in 1997 had a lower GSI (Figure 3), possibly because they did not have enough energy intake or reserves for vitellogenesis. Once eggs hatched at the end of May, the GSI for females that had reproduced increased (Figure 3). In southeastern Alaska, ovigerous females have significantly lower feeding rates than nonovigerous crabs in laboratory studies (Schultz

and Shirley, 1997). In this study, nonovigerous females were feeding more than ovigerous females (personal observations). Thus, nonovigerous females had more energy to invest in vitellogenesis.

The GSI of females that had reproduced in 1997 reached the same level by October 1998 as females that did not reproduce, before their GSI decreased in October (Figure 3). At the end of the study 38% (3 of 8) of the crabs that reproduced in 1997 also extruded eggs in 1998. Lobsters in aquaria, which are fed to excess and live in ideal conditions, reproduce more frequently than wild lobsters (Kanciruk, 1980). When food is not limiting, as in this study, Dungeness females may be able to reproduce annually. It is not known if the remaining 5 crabs that reproduced in 1997 also would have extruded eggs in 1998 since they were sacrificed in October. The GSI of these crabs were relatively high and ranged from 17% to 24.07% which may suggest that egg extrusion would have occurred, but GSI could have also dropped among these five females as it did among females that did not reproduce in 1997.

Egg Extrusion and Hatching

In the last month of this study, a higher percentage of females that did not reproduce in 1997 extruded eggs in 1998 when compared to females that reproduced in 1997 (47% vs. 38%). It appears as if females do not simply reach an age in which they stop reproducing, instead, they can skip at least one reproductive season and then reproduce in another season. Approximately half of the females that did not reproduce in 1997 reproduced in 1998, thus skipping at least one season. The other half that did not extrude eggs in 1997 or 1998 may have extruded eggs in a following season.

Females were collected in the field and brought into the laboratory beginning in October 1997. Some of the females were collected in an ovigerous state (70%), thus extruding eggs before collection. Once in the laboratory, females extruded eggs until the end of January. Fourteen percent of the females that reproduced in 1997 extruded eggs in November, 8% in December and 8% in January (Appendix 4). All of the ovigerous females reared in the laboratory hatched eggs during the last week in May. Although egg extrusion does not appear to be synchronous, egg hatching appears to be highly synchronous.

Observations on the Occurrence of Blackened Pleopods in the Laboratory

Setae of female crabs becomes matted or blackened after eggs have hatched. This condition of matted or blackened setae has been used as an indicator of female reproduction. A female is assumed to have recently brooded eggs and not molted if she has blackened setae. In this study, none of the females that hatched eggs in the laboratory developed blackened setae. The crabs were held in a sediment free, clean environment that may have prevented setae from becoming matted or blackened.

Effects of Latitude and Environmental Conditions on Crustacean Reproduction

Changes in water temperature and photoperiod are suggested to be cues in reproductive events of crustaceans (Waddy and Aiken, 1991; Talbot and Helluy, 1995). Temperature controls secondary vitellogenesis and photoperiod controls primary vitellogenesis in the spider crab *Acanthonyx lunulatus* (Chaix, 1984). American lobster eggs hatch when the water temperature warms (Waddy and Aiken, 1991), and an increase in water temperature is known to significantly accelerate gonadal development in many

species, including the spiny lobster (Lipcius and Herrnkind, 1987). If water temperature does not increase enough, the American lobster will not extrude eggs (Waddy and Aiken, 1991). Water temperature can play a vital role in determining egg development rates. The duration of embryonic development of *Chionoecetes opilio* is one year in warmer water and two years in colder water (Moriyasu and Lanteigne, 1998). Photoperiod can regulate vitellogenesis and egg extrusion, especially when temperature remains relatively uniform throughout the year (Waddy and Aiken, 1991; Talbot and Helluy, 1995).

In this study, water temperature began to increase in May (Figure 3, Appendix 2), at the time photoperiod was also increasing dramatically. Increases in water temperature or photoperiod may have cued egg hatching. After egg hatching, GSI began to increase in both groups of females. The hatching of eggs may be a cue for non-reproducing females to invest more energy into vitellogenesis or to advance from primary vitellogenesis to secondary vitellogenesis, but females that reproduced in 1997 and those that did not reproduce in 1997 were reared in separate tanks. Therefore, egg hatching probably was not the cue for increased gonad development investment. Water temperature was highest in August and September (Appendix 2), when most of the crabs extruded eggs in the laboratory. GSI increased steadily in both groups through September. In October water temperature began to decrease slightly and photoperiod was also decreasing. At this time, GSI continued to increase for females that reproduced in 1997 and decreased significantly for females that did not reproduce (Figure 3).

Resorption of Gonads and Utilization of Stored Sperm Among Crustaceans

The significant decrease in GSI from September to October 1998 among females that did not reproduce in 1997 (Figure 3) was unexpected. The decrease could be caused by one of two factors: resorption of gonads or an increase in body weight. A comparison of dry gonad size by carapace width increases in almost every instance as the year continued, until the month of October. In the month of October, dry gonad weight was substantially smaller for individual carapace width when compared with September gonad values. It would be expected that dry gonad weight would increase in October, such as was seen in the previous months. Furthermore, body weight would have to increase quite a bit to cause the decrease in GSI seen. Body weight did not increase substantially between September and October. Comparisons in gonad and body weights between September and October suggest that gonads were indeed resorbed and that the decrease in GSI was not the result of increased body weight.

Resorption of gonads has not been documented in Dungeness crabs. Gonadal resorption has been observed in a few crabs incidentally, as was the case in this study. Research has not been conducted that specifically examines gonadal resorption among crabs. Resorption of unspawned mature eggs in the ovaries of red king crabs have been observed (Matsuura *et al.*, 1971; McMullen and Yoshihara, 1971; Otto *et al.*, 1989). Histological inspection of one female red king crab found that both nearly mature and immature gonads were resorbed (Matsuura *et al.*, 1971). Immature oocytes of blue king crabs appeared to remain intact but oocytes that underwent vitellogenesis but did not reach maturity may have been resorbed (Jensen *et al.*, 1985). Resorption of oocyte

vitellin is common among the American lobster and is thought to occur during secondary vitellogenesis (Waddy and Aiken, 1991).

The resorption of gonads seen in this study does not appear to be a laboratory effect because a significant decrease in GSI was also observed in crabs collected in the field between September and October (Figure 4). Females may resorb their gonads if they did not reproduce by a certain time. Gonads in non-reproducing females may follow a cyclical pattern in southeastern Alaska and remain around a GSI of 10% for most of the year and increase from July through September in anticipation of mating. If the females do not mate, then gonads may be resorbed until the next year.

Numerous crustacean species are able to store viable sperm that can fertilize subsequent egg clutches without mating. Dungeness crabs can store and utilize sperm for at least 2.5 years (Hankin *et al.*, 1989). A laboratory study of snow crabs, *Chionoecetes opilio,* suggested that sperm stored in the first mating can fertilize a second egg clutch (Sainte-Marie and Carriere, 1995), and that snow crabs do not extrude eggs when the ratio of sperm per oocyte is lower than 7:1 (Sainte-Marie and Lovrich, 1994). Female snow crabs can undergo different reproductive pathways including utilizing stored sperm or copulating (Elner and Beninger, 1995). Female Dungeness crabs may also undergo similar reproductive pathways. In northern California, female Dungeness crabs extrude eggs annually without annual molting and mating, thus relying on stored sperm (Hankin *et al.*, 1989)

The laboratory females in this study may have already used their stored sperm reserves and were unable to extrude a fertilized egg clutch since they were isolated from

males, although it seems unlikely for all the females in the study. Female Tanner crabs have been found to not extrude eggs, or to extrude unfertilized eggs when isolated from males for more than one breeding season (Paul, 1984). The females collected from the field should not have been isolated from potential mates, but they resorbed gonads as well. The decrease in water temperature may have cued the females that the reproductive season had ended and the crabs that had not extruded began to resorb their gonads in preparation for the next season (Appendix 3).

Determination of Sampling Artifacts and Laboratory Effects

It was assumed that only mature crabs were used in this study as described in the material and methods, but it should be stated that sexual maturity of crabs was not specifically determined for the crabs utilized. The differences in gonad development in this study may have been the result of comparing immature crabs (those without eggs) with mature crabs (those with eggs). I believe that this is highly unlikely since many researchers have evidence suggesting that female Dungeness crabs mature at approximately 93 through 100 mm CW (Butler, 1960, Orensanz and Galluccci, 1988, Swiney, 1999) and only females 106 mm CW and larger were used in this study.

To determine if there were significant laboratory effects, crabs were collected from the field periodically and compared to laboratory reared crabs. This comparison was not completely valid among the female crabs because the recent reproductive history of the field female crabs was unknown. All or none of the female crabs from the field could have reproduced in 1997. Most likely they represent both groups, but it was not possible to confirm reproductive status. The GSI of females from the field in April was

significantly different and highly significantly different in July compared to nonovigerous laboratory females (Figure 4, Table 1), but this may be due to lumping all females from the field together. September and October field and laboratory females GSI were not significantly different (Figure 4, Table 1). There was not a significant difference between the laboratory and field GSI of ovigerous females (Table 1).

GSI was significantly higher for laboratory reared males than males from the field in October (Table 1). Higher GSI of laboratory reared males may have been the result of a laboratory effect because crabs were fed *ad libitum*, which may have inflated GSI at the end of the study.

The large increase in GSI between September and October among females that reproduced in 1997 may be the artifact of a small sample size since only 2 crabs were sacrificed in September. The increase in GSI may also be a laboratory effect. Crabs were fed *ad libitum*, which may not occur in the wild. It was not possible to test for a laboratory effect by comparing field and laboratory crabs since the reproductive histories of the field crabs were unknown. Even if the GSI values, especially for September, were an artifact of a small sample size, the pattern of increased GSI appeared to be a true pattern.

Laboratory effects were probably insignificant in this study. The ability of a crab to extrude eggs did not appear to be hampered by being reared in the laboratory. Numerous crabs extruded eggs in the laboratory, both when they were initially collected and during the last few months of the experiment. Some females may not have extruded eggs at the end of the experiment because their reserve of stored sperm was depleted;

however, the crabs probably were not held long enough for this to be a concern since stored sperm has been reported to be viable for at least 2.5 years (Hankin *et al.*, 1989). More likely, the crabs did not extrude eggs because it was not the year in their reproductive cycle to reproduce.

Comparison of Gonadosomatic Index and Oocyte Measurements

GSI and oocyte areas were significantly higher for females that did not reproduce in 1997 when compared to females that did reproduce in 1997 (Figure 3; Figure 5). GSI and oocyte areas produced similar trends of gonad development among both groups of females (Figure 6; Figure 7). In general, oocyte areas increased steadily, whereas GSI remained about the same for the first 3 months both among females that reproduced and among those that did not (Figure 6; Figure 7). The apparent discrepancy between GSI and oocyte measurements can be explained by the nature of the two indexes. Individual oocytes can be constantly increasing in area through vitellogenesis, hence the steady increase seen in the data, but it would take a substantial increase in oocyte size to be detected by GSI.

October was interesting because oocyte area continued to increase a little, although not significantly among females that did not reproduce in the laboratory, but GSI decreased significantly (Figure 6). The decrease in GSI suggests resorption of gonads. The increase in oocyte area may be a result of laboratory effect because mean oocyte area was highly significantly less for field crabs than those in the laboratory for the month of October (Table 1). Resorption of gonads may not have been detected in oocyte area data because only intact oocytes were measured. This study was not

designed to detect resorption at the individual oocyte level. A closer examination of gonads, such as a histological approach, may detect resorption of individual oocytes.

Females that reproduced in 1997 had more similar trends in GSI and oocyte size than females that did not reproduce in 1997 (Figure 9). Throughout most of the study, females that reproduced had low GSI and oocyte area with less variance, whereas females that did not reproduce had higher GSI values, oocyte areas and variance.

Gonad Development Studies in the Future

In the future, sacrificing Dungeness crabs to determine their stage of gonad development and GSI may not be necessary. Because there was a correlation between oocyte area and GSI, in theory, GSI can be derived by obtaining a sample of oocytes without sacrificing the crab. A biopsy approach has obvious advantages. The crabs would not have to be sacrificed so changes in gonad development for an individual crab could be tracked over a long period of time. Many questions could be answered such as, if a crab reaches a certain GSI level do they always extrude eggs? How high does GSI have to be before a crab extrudes eggs? With this method one could also determine more directly if females resorb gonads. Although this method is promising, there are potential problems. Months like October would pose a problem because oocyte area is large and GSI would be expected to be higher, but GSI decreased in October. Likewise, a scattergram reveals a group of crabs with high GSI and low oocyte area (Figure 8). If the oocytes were measured for these crabs then a lower GSI would have been extrapolated. For example, a crab with an oocyte area of 0.1 mm can have a GSI of approximately 0%

up to 15%. I believe that even with the possible problems this method may encounter, it can still be a valuable tool in obtaining information on gonad development.

Monitoring of hormonal levels may also be useful in determining stages of gonadal development without sacrificing the study animal. The hormone methyl farnesoate is synthesized by the mandibular organs, is thought to be important in reproduction (Laufer *et al.* 1987) and is secreted into the hemolymph (Reddy and Ramamurthi, 1998). The amount of methyl farnesoate in the hemolymph varies depending on development stage, gender, and sexual maturity. The production of methyl farnesoate increases during vitellogenesis and then decreases to pre-vitellogenic levels when the oocytes mature for both *Cancer paguraus* (Wainwright *et al.*, 1996) and *Libinia emarginata* (Laufer *et al.*, 1987). Methyl farnesoate also stimulates ovarian maturation in the crab *Oxiotelphusa senex senex* (Reddy and Ramamurthi, 1998). Methyl farnesoate, or other hormones, may one day be vital in determining the stage of gonad development based upon levels of the compound in hemolymph.

Comparisons of Crustacean Reproductive Cycles

The reproductive cycle of the American lobster has been well documented. Reproduction in the American lobster is very similar to Dungeness reproduction; for example, both species retain sperm and brood eggs. The reproductive cycle of the American lobsters is synchronized. Smaller females spawn every other year. Females larger than 120 mm carapace length spawn more frequently, often three times in five years (Waddy and Aiken, 1991; Waddy *et al.*, 1995). Females over 120 mm carapace length often spawn twice without molting. This consecutive spawning can occur in two

forms. In successive-year spawning the females spawn in two successive summers and in alternate-year spawning the females spawn in alternate summers (Waddy and Aiken, 1991; Waddy and Aiken, 1995). Variations in the reproductive cycle of lobsters are common at the northern and southern ends of their range where water temperatures are not ideal for reproduction (Waddy *et al.*, 1995).

Populations of species may vary in duration and frequency of reproductive cycles in different parts of their range, especially those populations occurring at higher latitudes (Sastry, 1983). Dungeness crabs are similar to other crustacean species in which different reproductive pathways can be followed. At the northern limit of its distribution, the crab *Eriphia smithii* was found to have three varied reproductive strategies shown by individuals (Tomikawa and Watanabe, 1992). The snow crab, *Chionoecetes opilio,* can also follow different reproductive pathways by either copulating in soft or hard shelled condition or utilizing stored sperm (Elner and Beninger, 1995). Likewise, female Dungeness crabs may either copulate in the soft-shelled condition or use stored sperm. There is some preliminary evidence that some Dungeness females may mate in hard-shell condition (T. Shirley, personal observation). The pathways that Dungeness crabs pursue may be dependent on environmental conditions such at latitude, water temperature or photoperiod.

In this study, the significant differences between GSI and oocyte measurements in laboratory females that did and did not reproduce in 1997 suggest that egg extrusion is not an annual event in southeastern Alaska. Similar conclusions have been drawn for other crab species. Even if the recent reproductive history of the crabs is not known, but

two groups of females at different gonad development states are present, the population is assumed to not reproduce annually. The false southern king crab, *Paralomis granulosa*, has two separate developmental groups of females and biennial reproduction was assumed due to differences in GSI and oocyte diameter in almost all sampled months (Lovrich and Vinuesa, 1993). Similar results have been found for the blue king crab in Alaska. Based upon 2 stages of gonad development discovered by histological examination, female blue king crabs, *Paralithodes platypus,* from the Pribilof Islands are thought to reproduce biennially and are unable to produce mature ovaries in one year (Jensen *et al.,* 1985). Similarly, blue king crabs from the western Bering Sea may reproduce biennially (Sasakawa, 1975).

The results of this study are in contrast to a study conducted on Dungeness crabs in central and northern California. In California, gonad development began immediately after egg extrusion while the crabs were brooding eggs (Wild, 1983a). This was not found in this study with Alaskan crabs. Alaskan females did not begin developing gonads until after eggs hatched in May (Figure 7). Alaskan crabs extrude eggs later (Wild, 1980) and eggs develop more slowly in colder water (Wild, 1983b). Wild suggested if gonad development does not begin until after eggs hatched that there would be significant differences in ovary development (1983a); which is what occurs southeastern Alaskan Dungeness crabs. The California results might be expected because the water is warmer and all of the processes are faster than in the colder waters of Alaska. In California, all female Dungeness crabs held in the laboratory extruded eggs (Wild, 1980), and were able to reproduce annually (Wild, 1983a).

Conclusions

All mature female Dungeness crabs in Alaska do not reproduce annually. In this study a large number of crabs were monitored that did not reproduce in 1997. Examination of data from a long-term project at Glacier Bay National Park and Preserve which included crab pot, dive and tagged crab data also suggests that females do not reproduce annually in Alaska (Swiney 1999). However, in the laboratory some females can reproduce in successive years. The reproductive cycle of Dungeness crabs in southeastern Alaska is complex, in part because females are able to extrude fertilized eggs without mating, by relying on stored sperm.

Throughout the study, females that did not reproduce in 1997 had significantly higher GSI and oocyte areas than females that did reproduce in 1997, until the month of October. In October, females that did not reproduce in 1997 appear to have resorbed gonads, where as females that reproduced in 1997 did not. Ovigerous females in Alaska do not invest energy into vitellogenesis until after egg hatching, in which time GSI and oocyte areas began to increase. Egg extrusion does not appear to be synchronous and egg hatching appears to be relatively synchronous. Male Dungeness crabs in southeastern Alaska also undergo seasonal gonad development.

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Figures

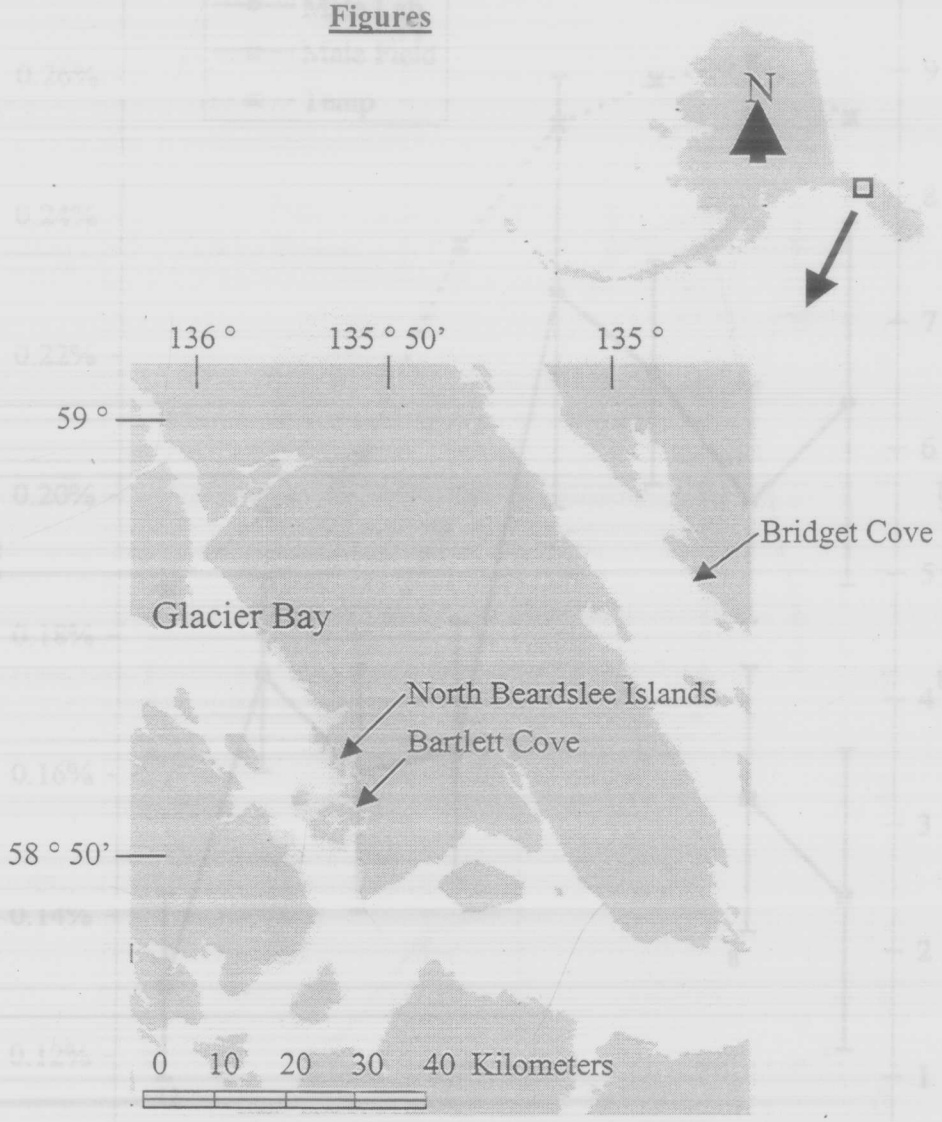

Figure 1. Locations where Dungeness crabs were collected for reproductive study. Females were collected from Bridget Cove which is located near Juneau, Alaska. Male Dungeness crabs were collected from Bartlett Cove and North Beardslee Islands which are located within Glacier Bay National Park and Preserve.

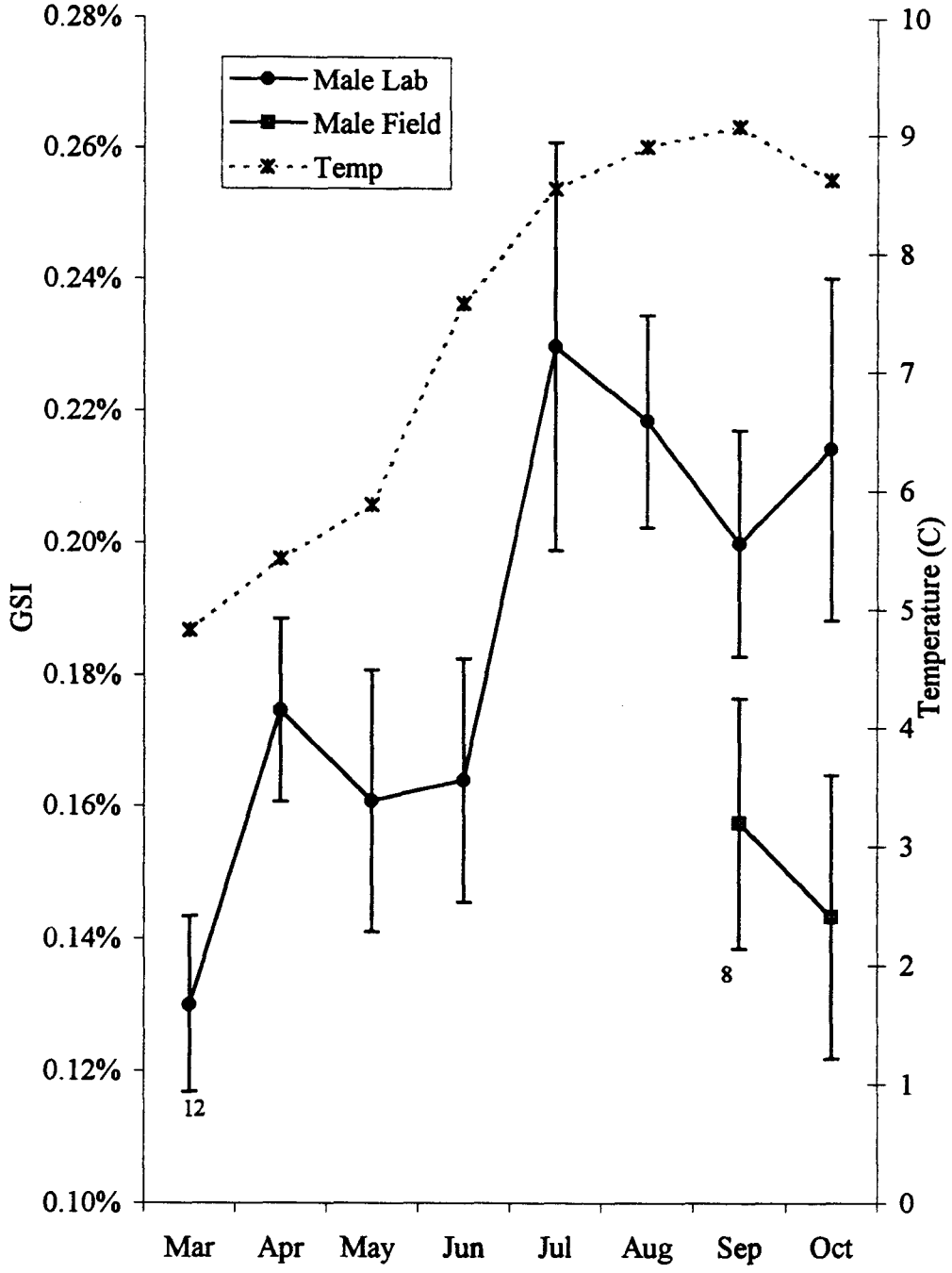

Figure 2. Gonadosomatic index (GSI) of field and laboratory reared male Dungeness crabs. Values are means ± one standard error (SE). Sample size is 10 every month except where noted. Temperatures represent means of weekly measurements.

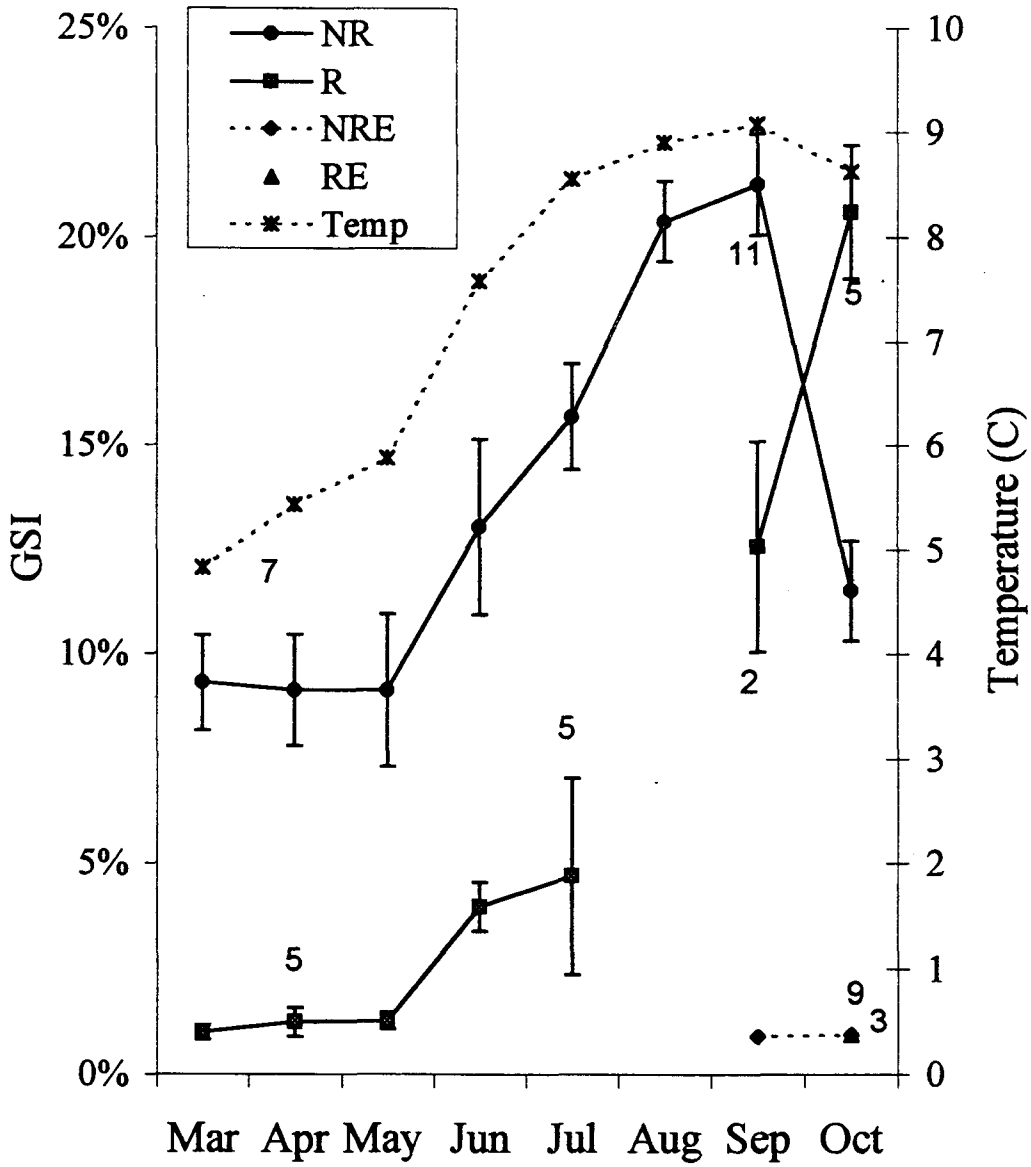

Figure 3. GSI of laboratory reared female Dungeness crabs. Values are means ± one standard error. NR = females that did not reproduce in 1997; R = females that reproduced in 1997, NRE = females that did not reproduce in 1997 and extruded eggs in 1998; RE = females that reproduced in 1997 and 1998. Sample size is 10 every month except as noted. Temperatures represent means of weekly measurements.

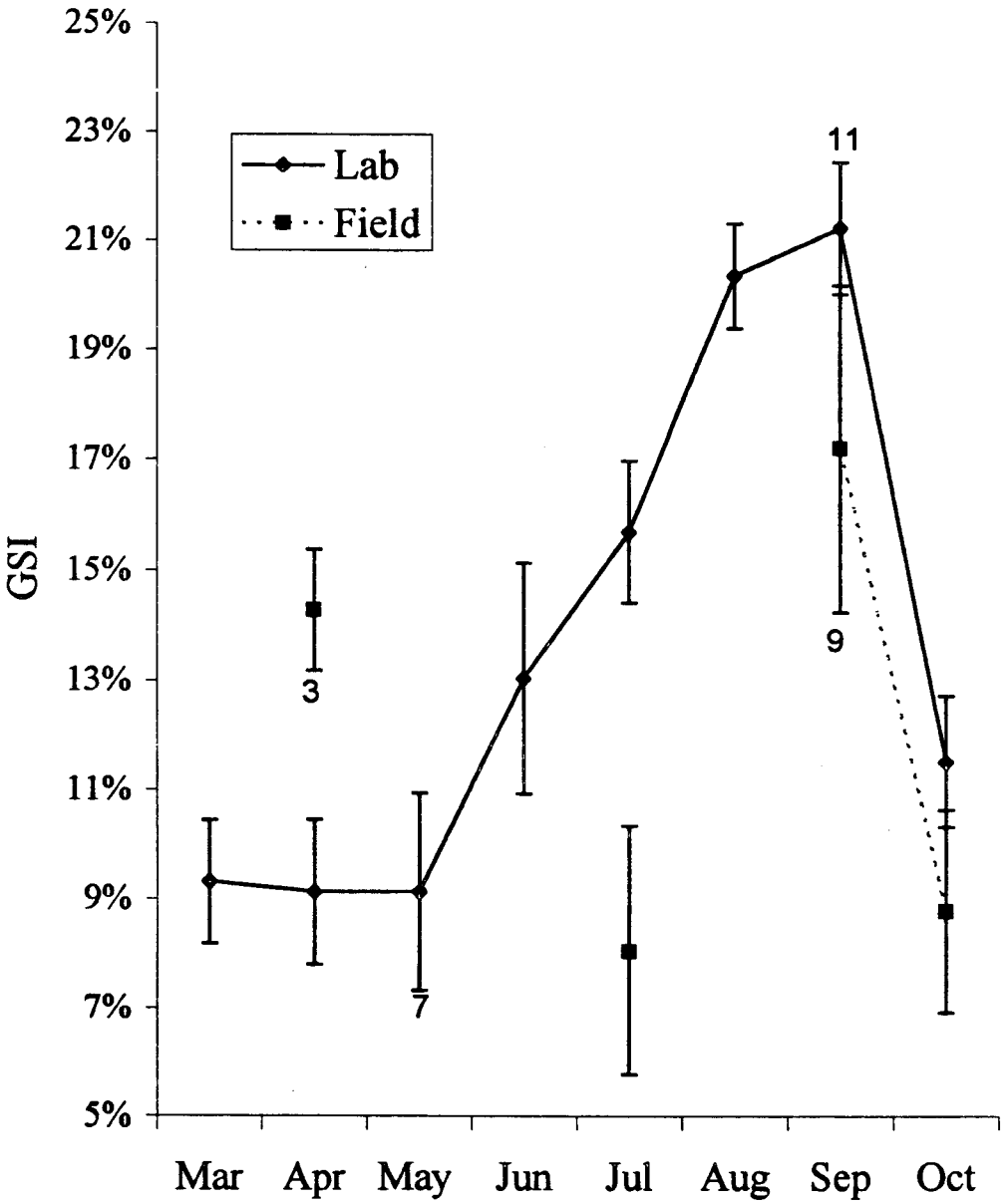

Figure 4. GSI of nonovigerus field and laboratory reared females. Values are means ± one standard error. Sample size is 10 every month except were noted.

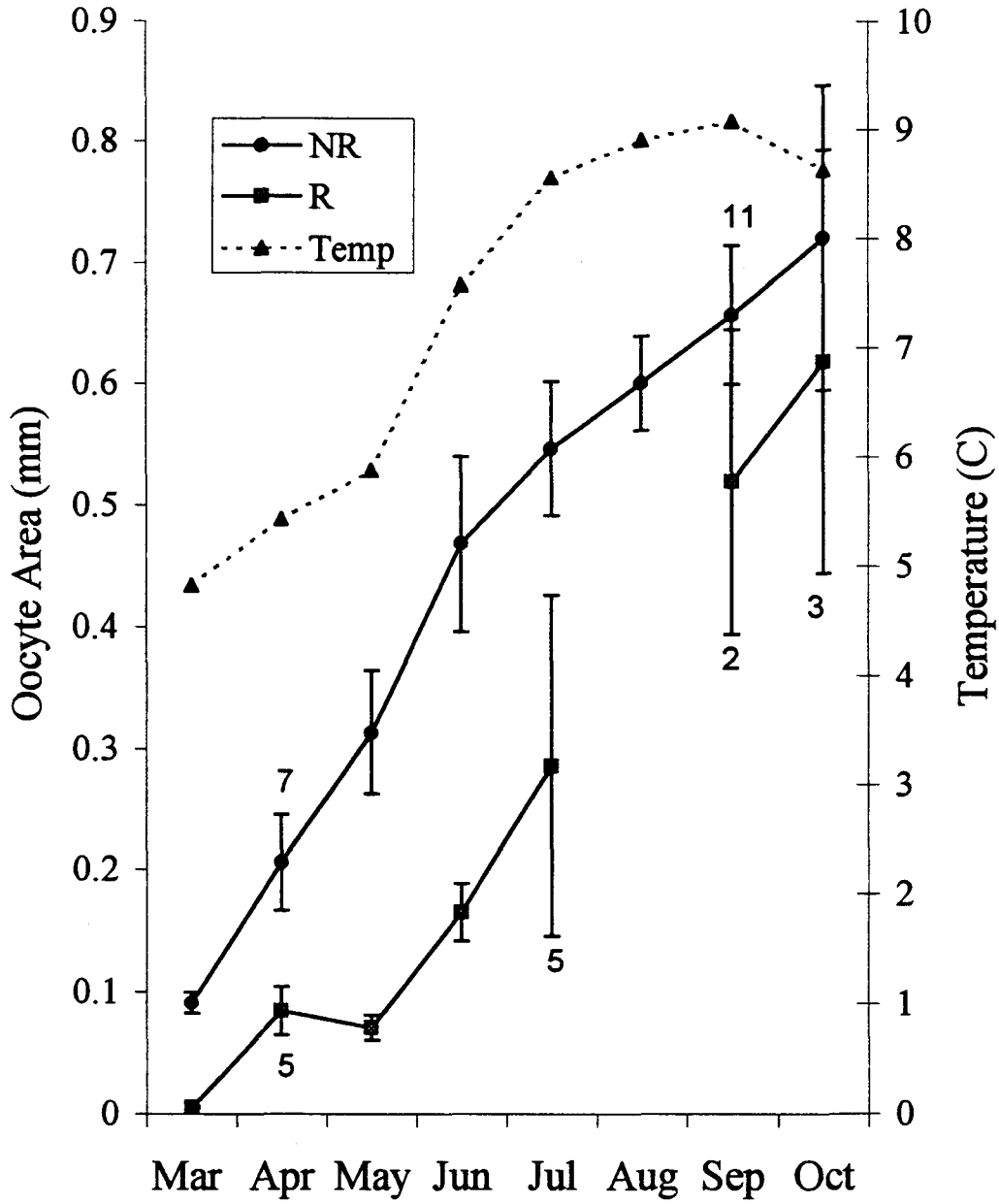

Figure 5. Mean oocyte areas of laboratory reared female Dungeness crabs. Values are means ± one standard error. NR = females that did not reproduce in 1997; R = females that reproduced in 1997. Twenty oocytes were measured per crab sacrificed. Sample size is 10 every month except as noted. Temperatures represent means of weekly measurements.

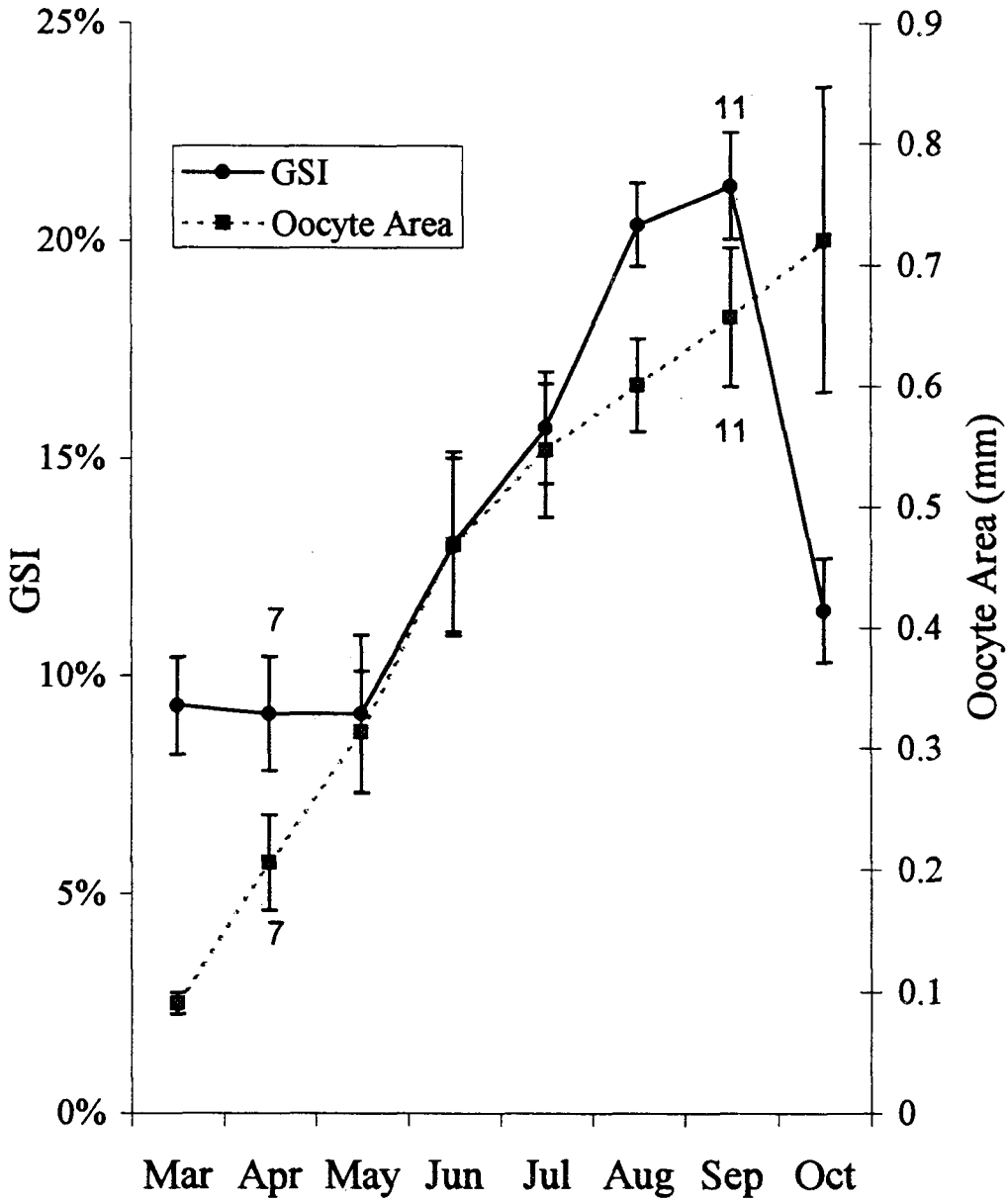

Figure 6. Comparison of GSI and oocyte area of females reared in the laboratory that did not reproduce in 1997. Twenty oocytes were measured per crab sacrificed. Sample size is 10 crabs every month except where noted. Values are means $\pm$ one standard error.

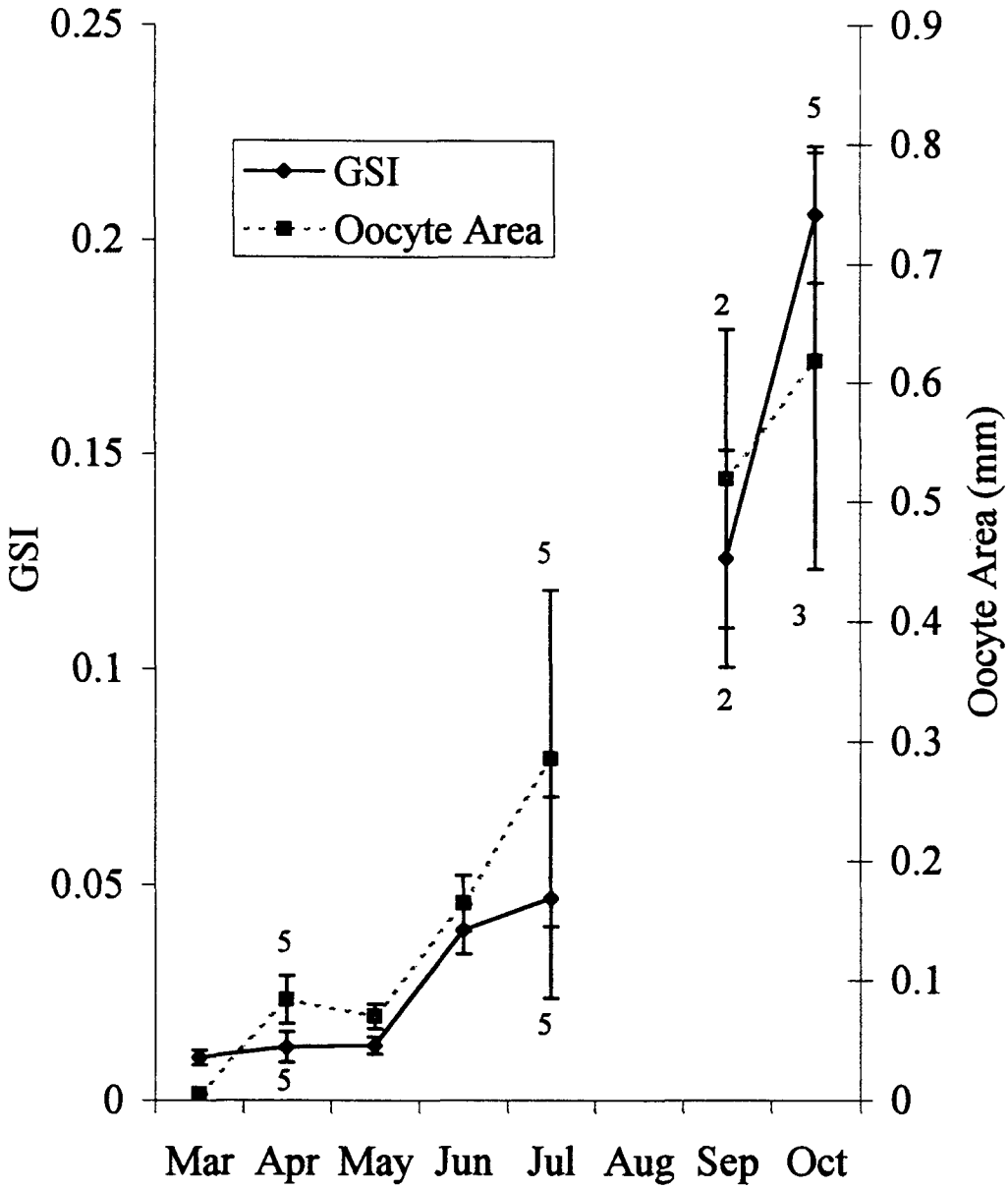

Figure 7. Comparison of GSI and oocyte area of females reared in the laboratory that reproduced in 1997. Twenty oocytes were measured per crab sacrificed. Sample size is 10 crabs every month except where noted. Values are means $\pm$ one standard error.

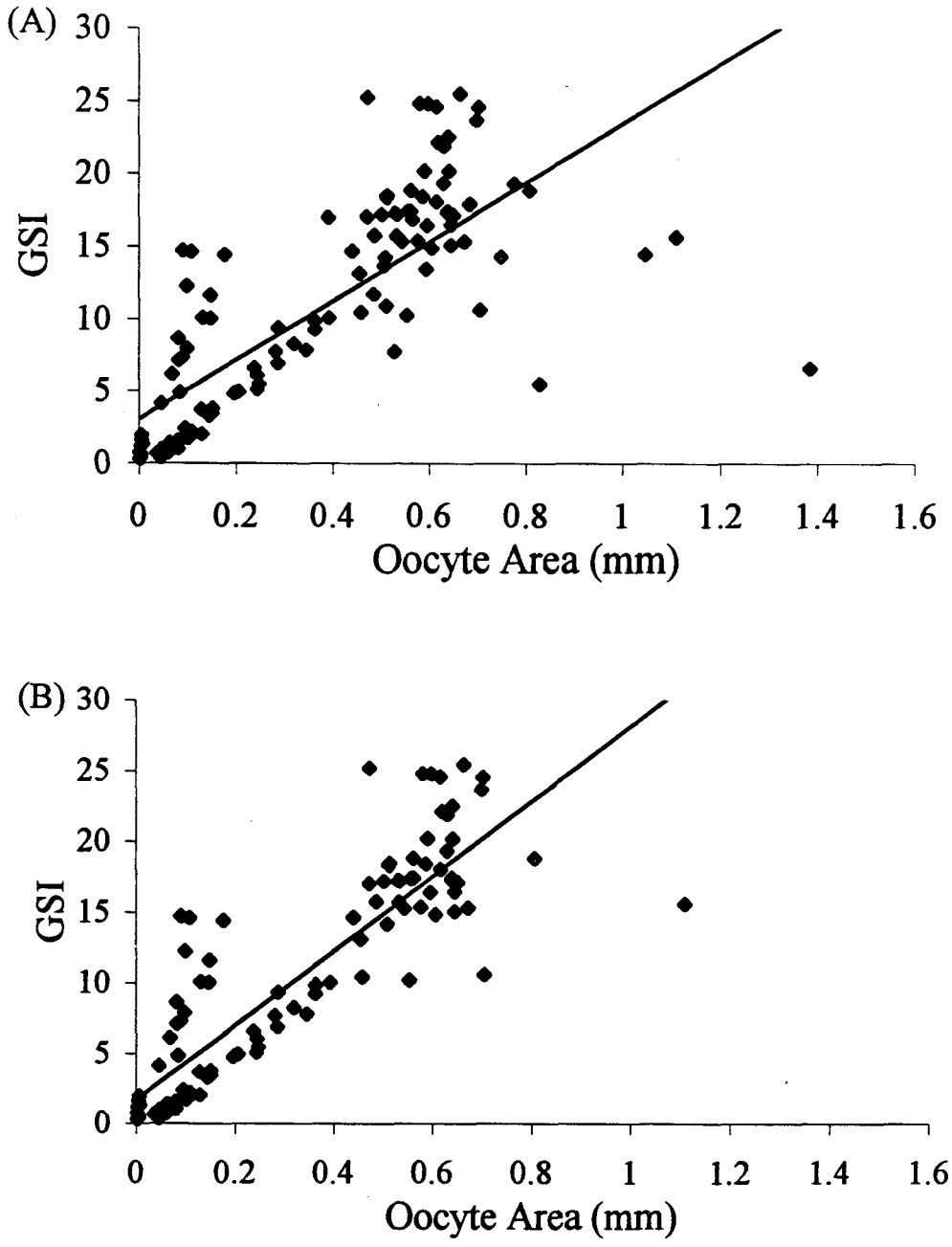

Figure 8. (A) Scattergram of GSI and oocyte area of all females from the laboratory. Correlation coefficient p=0.763. Sample size is 123. (B) Scattergram of GSI and oocyte area of all females from the laboratory, excluding October data. p=0.871. Sample size is 110.

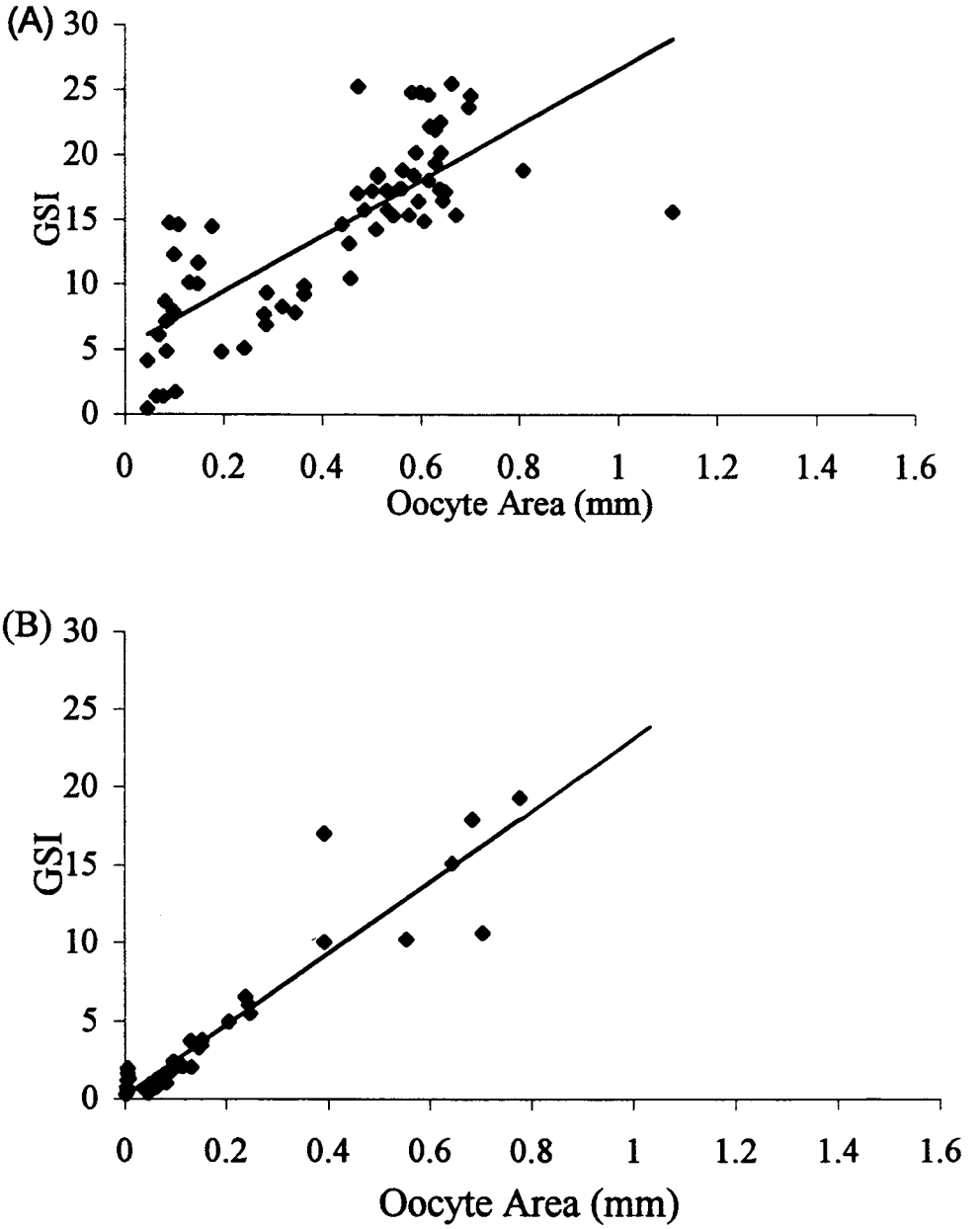

Figure 9. (A) Scattergram of GSI and oocyte area of laboratory females that did not reproduce in 1997, excluding October. Correlation p =0.784. Sample size is 68. (B) Scattergram of GSI and oocyte area of laboratory females that did reproduce in 1997. p =0.942. Sample size is 45.

Tables

Table 1. Comparison of laboratory and field data with respect to GSI and oocyte area for male, ovigerous and nonovigerous Dungeness crabs. Top values are mean GSI or oocyte area and values in parentheses are standard errors. T-test results are considered significant when P<0.05 (*) and highly significant when P<0.01 (**).

GSI	Lab	Field	t-stat	P-value
Male				
Sept	0.002	0.002	1.311	
	(<0.001)	(<0.001)		
Oct	0.002	0.001	2.106	*
	(<0.001)	(<0.001)		
Ovigerous Female				
April	0.012	0.009	0.761	
	(0.003)	(0.001)		
Oct	0.009	0.011	-0.706	
	(0.016)	(0.003)		
Non-ovigerous Female				
April	0.091	0.143	-2.351	*
	(0.013)	(0.011)		
July	0.157	0.08	2.917	**
	(0.013)	(0.023)		
Sept	0.207	0.169	1.255	
	(0.012)	(0.029)		
Oct	0.115	0.088	1.243	
	(0.012)	(0.019)		
Oocyte Area				
Ovigerous Female				
April	0.084	0.079	0.237	
	(0.019)	(0.014)		
Non-ovigerous Female				
April	0.206	0.335	-1.475	
	(0.039)	(0.101)		
July	0.547	0.267	3.78	**
	(0.055)	(0.062)		
Sept	0.657	0.514	1.544	
	(0.057)	(0.091)		
Oct	0.72	0.315	3.643	**
	(0.126)	(0.059)		

CHAPTER 2: REPRODUCTION IN FEMALE DUNGENESS CRABS: AN *IN SITU*, MULTI-YEAR STUDY

Prepared for submission to the Journal of Crustacean Biology

Abstract

Not all mature female Dungeness crabs in Alaska reproduce annually. Numerous variables, such as crab size, shell condition, appendage injury, crab depth distribution and catchability were compared between nonovigerous and ovigerous females and between spring and fall seasons to explain why all females are not extruding eggs annually. Presence and size distribution of females with blackened pleopods, an indicator that a female had brooded eggs and not since molted, were also examined. Crabs collected from five bays within or near Glacier Bay National Park and Preserve, Alaska were studied from 1992-1998. Two sampling methods, baited crab pots and dive transects, were utilized in the spring (April) and fall (September) of each year. A large percentage of nonovigerous females were observed in the spring samples (86% pots, 35% SCUBA), a time in which females should be brooding egg clutches. In spring samples, ovigerous females were significantly smaller than nonovigerous females ($\mu = 145.4 \pm 0.7$, $\mu = 149.3 \pm 0.3$ respectively). The largest proportions of females with blackened pleopods were between 141-170 mm CW. These larger females do not molt annually and may either rely on stored sperm to fertilize egg clutches or may wait until they molt and mate before extruding eggs. Proportionally more ovigerous females had damaged appendages than nonovigerous females; the damage may have been caused during mating. Missing or regeneration of limbs did not appear to negatively affect egg extrusion. A long term tagging study revealed that some females skipped at least one mating season and extruded eggs at a later time without molting. Large females probably do not extrude eggs annually due to lower molting probabilities, which limits mating potential, but

females can rely on stored sperm to fertilized eggs. A modified reproductive cycle of Dungeness crabs in Alaska is introduced.

Introduction

Dungeness crabs, *Cancer magister*, support important commercial fisheries from central California to Kodiak, Alaska. Southeastern Alaska has been a large contributor to the total Alaskan landings and in 1996 and 1997 this area contributed 81% of the total Alaskan catch. In 1997, the ex-vessel value of the Dungeness fishery in Alaska was $11,098,114 (personal communication S. Shirley, State of Alaska Commercial Entry Fisheries Commission). In Alaska, the Dungeness crab fishery is managed on a 3-S system: sex, size and season. Only male Dungeness crabs greater than 165 mm in carapace width may be retained in the Alaskan fishery within predetermined seasons (Alaska Department of Fish and Game, 1998).

Dungeness crabs are distributed from the Pribilof Islands, Alaska to Santa Barbara, California (Jensen, 1995). They most commonly inhabit sandy or muddy sand areas, but are found on almost any substrate (MacKay, 1943; Cleaver, 1949; Hipkins, 1957; Hoopes 1973) in bays, estuaries and open ocean near the coast (Hoopes, 1973). Dungeness crabs range from the intertidal (Hart, 1982) to at least 200 meters (T. Shirley, unpublished data).

Mating in *Cancer magister* occurs between hard-shelled males and recently molted females that are in a soft-shelled condition (MacKay, 1943; Butler, 1960; Snow and Neilsen; 1966; Hoopes, 1973). After copulation, sperm is stored in paired spermathecae and months to years later eggs are fertilized as they pass by the

spermathecae during extrusion (Jensen *et al.*, 1996). The eggs form a spongelike mass, adhering to the setae on the pleopods where they are brooded until hatching (Wild 1980; Jaffe *et al.*, 1987). *Cancer magister* in southeastern Alaska begin mating and extrude eggs from September through November (Shirley *et al.*, 1987). The eggs hatch April through August with most of the hatching occurring in May and June (Shirley *et al.*, 1987).

Crustaceans generally have one of two reproductive strategies. In a synchronously mating population all females are ovigerous at the same time and mating is usually restricted to a short period. At any time of the year all ovaries or eggs will be in about the same stage of development (Sastry, 1983). Asynchronous mating within a specific time of the year is common in crustaceans from temperate, subtropical and tropical regions. Females in these populations are usually out of phase, but the population as a whole begins and ends mating at the same time. Asynchronicity can result from the production of several clutches by the females or by production of a single clutch by each female out of phase (Sastry, 1983). Generally, crustaceans with planktotrophic larvae linked with peak primary production mate synchronously in higher latitudes and asynchronously or continuously in lower latitudes (Sastry, 1983). Based upon literature, it is predicted that Dungeness crabs in Alaska would mate synchronously.

Dungeness crabs are generally thought to extrude eggs annually (Wild, 1983; Jaffe et al., 1987), but this is not true for all mature female Dungeness crabs in southeastern Alaska (Swiney, 1999). Alaska is the northern limit of the range for Dungeness crabs, and this may affect the periodicity of reproduction. Different

populations of the same species may vary in duration and frequency of reproductive cycles in different areas of their range, especially those occurring at higher latitudes (Sastry, 1983). Water temperature, diet, photoperiod and other environmental conditions have been linked to changes in periodicity and timing of mating and egg production in many crustaceans. Variations in the reproductive cycle of lobsters, for example, are common at the northern and southern ends of their range where water temperatures are not optimal (Waddy *et al.*, 1995). In general, species inhabiting cold waters (<10°C) have much longer embryogenic periods than those living in warmer water because low water temperatures decrease the rate of embryogenesis (Shirley *et al.*, 1987; Shields, 1991).

Gamete production requires energy and an organism must allocate energy to this process in order to reproduce (Sastry, 1983). In addition to the cost of gamete production, ovigerous female Dungeness crabs have significantly lower feeding rates and foraging responses than nonovigerous females in Alaska (Schultz and Shirley, 1997) and may not have sufficient energy to allocate to gonad production until after egg hatching. Therefore, gonads may not have enough time to develop before the next mating season. Sixty-seven percent of 587 mature females collected during a study throughout southeastern Alaska during May 1982 and April 1983 were ovigerous (O'Clair and Freese, 1988). If all mature females were extruding eggs annually a higher percent of ovigerous females would be expected.

A laboratory study provided evidence that all females in Alaska do not reproduce annually. Females were collected and observed in the laboratory for a year and a large

portion of the females did not extrude eggs (Swiney, 1999). Gonadosomatic indexes and oocyte measurements were significantly higher for females that did not reproduce for the year when compared to females that did reproduce, suggesting different gonad development rates between the two groups. The females that did extrude eggs for the season did not begin developing gonads until after egg hatching (Swiney, 1999).

Knowledge of Dungeness crab biology can be utilized to examine reproductive cycles of these crabs. Examination of many variables together and separately might be useful in determining why some females extrude eggs in a given year and others do not. An examination of carapace size might suggest that larger or smaller females were not reproducing annually. Blackened pleopods are an indicator that a female that carried an egg clutch has not molted since the eggs hatched; thus examination of the pleopods could be useful. The size distribution of females with blackened pleopods might indicate that certain size classes brood an egg clutch and then wait for a year or two before molting, mating and producing a subsequent egg clutch.

Appendage damage and carapace condition have been used to examine the reproductive status and potential of crabs (Abello *et al.*, 1994; Durkin *et al.*, 1984; Jensen *et al.*, 1985; Sekkelsten, 1988; Hankin *et al.*, 1989; Smith, 1992; Lovrich and Vinuesa, 1993; Sainte-Marie, 1993; Juanes and Smith, 1995; Paul *et al.*, 1995; Wilber, 1995). Appendage injury such as damaged, missing and regenerating limbs has not been examined often in female crabs, but trade-offs may exist between fecundity and regeneration of limbs for female crabs (Juanes and Smith, 1995). *Chionoecetes opilio* males with larger chelae were found with females missing fewer limbs (Sainte-Marie *et.*

al., 1999). Missing appendages may be particularly important for species in which females reach a terminal molt. The number of limbs missing may have a direct impact on life expectancy and fitness for these species (Sainte-Marie *et. al.*, 1999). Missing or regenerating limbs may negatively affect the ability of crabs to feed, molt, attract mates, successfully mate and may reduce fecundity (Durkin *et al.*, 1984; Smith, 1992). Limb injury in crabs has been attributed to many causes including predation, agonistic interactions and commercial fishing practices (Durkin *et al.*, 1984; Wilber, 1995). Among females, damage may also be caused by courtship and mating activity (Juanes and Smith, 1995). Fewer male shore crabs, *Carcinus maenas,* with an injury such as a missing chela were found in mating pairs when compared to uninjured males in mating pairs (Sekkelsten, 1988; Abello *et al.*, 1994). Both male and female stone crabs with regenerating claws did not occur in mating pairs as frequently as expected (Wilber, 1995). Female stone crabs that were regenerating claws extruded eggs later in the reproductive season than females that were not regenerating limbs (Wilber, 1995). To date, no study has examined if there is a difference between the rate of nonovigerous and ovigerous females with missing, damaged or regenerating appendages at a given time to determine if appendage injury is a handicap for female crabs.

Shell condition has been utilized in determining reproductive dynamics among crab species (Jensen *et al.*, 1985; Sainte-Marie, 1993). Shell condition was found to be a useful indicator to determine if male Tanner crabs, *Chionoecetes bairdi,* were likely to mate (Paul *et al.*, 1995). Among Dungeness crabs, shell condition was used with other parameters to determine that females were able to rely on stored sperm to fertilize egg

clutches (Hankin *et al.*, 1989). Shell condition was also used as supporting evidence for biennial reproduction of the false southern king crab, *Paralomis granulosa* (Lovrich and Vinuesa, 1993). Shell condition could be used to estimate the time since a female had molted. If the majority of females found in a population were nonovigerous and very old shelled this would suggest that they were not molting and might be unable to produce an egg clutch. Whereas, if the nonovigerous females were new shelled, this would suggest that they have molted, probably within the year, but had not extruded eggs. Shell condition can be a valuable tool in assessing differences between nonovigerous and ovigerous crabs.

Data collected from a 7 year study, 1992-1998, in Glacier Bay National Park and Preserve, Alaska were analyzed in this study to further examine if female Dungeness crabs in Alaska reproduce annually. A variety of variables were analyzed to see if differences existed between ovigerous and nonovigerous females collected in the spring and fall samples to explain why some females do not reproduce annually. The objectives of this study were to:

(1) examine seasonal variations in catch rates of nonovigerous and ovigerous females by both crab pot and SCUBA sampling methods. Seasonal differences in catch rates between nonovigerous and ovigerous females may suggest in what season females extrude eggs. By examining both pot and SCUBA data, potential biases in sampling methods could be suggested.

(2) determine if ovigerous and nonovigerous females were found at different depth strata. Females move inshore to mate and extrude eggs.

(3) Compare size of nonovigerous and ovigerous females as well as the occurrence of blackened pleopods among nonovigerous females. Size comparisons of nonovigerous and ovigerous females can be very valuable in analyzing which group of females may not extrude eggs annually. Blackened pleopods can be used to further evaluate if certain size classes are not extruding eggs annually.

(4) Compare differences in appendage damage and injury among nonovigerous and ovigerous females. Appendage damage and injury may or may not be a handicap in egg extrusion and mating among females.

(5) Examine shell condition of nonovigerous and ovigerous females. Shell condition may also be vital to understanding what group of females may not be reproducing annually. A tagging study added additional data on recent reproductive activity of individual females.

Methods and Materials

Study Area

The study area included five bays in southeastern Alaska. Four of the bays - north Beardslee Islands (58°31'N, 135°54'W), south Beardslee Islands (58°30'N, 135°53'W), Berg Bay (58°31'N, 136°13'W), and Bartlett Cove (58°27'N, 135°53'W) - are located within Glacier Bay National Park and Preserve. The fifth bay, Gustavus Flats (58°23'N, 135°43'W), lies adjacent to the park's boundary (Figure 1).

Glacier Bay is a glacial fjord system with high sedimentation rates of silt-clay particles (Cowan, 1993). The bottom type is primarily silt with sand and occasional algal mats. Glacier Bay is 161 km long and 126 km at its widest point. The bathymetry of Glacier Bay ranges from shallower depths at the south end of the park to a maximum depth of 430 m in the central and northern portion.

Sampling Periods

Sampling was conducted biannually with spring sampling in April and fall sampling in September. These sampling periods were selected to avoid conflicts with the commercial fishery and to coincide with reproductive events of Dungeness crabs. April sampling occurs prior to larval hatching and before the commercial fishery opens in June. September sampling occurs during a time of mating and egg extrusion and when the commercial fishery is closed from August 15th to September 30th. Data were analyzed from the initiation of the project in April 1992 to fall 1998; no sampling occurred in the spring of 1998.

Crab Pot Sampling

Commercial crab pots were used for crab collection. Pots were baited with fresh hanging bait of halibut, salmon or cod and perforated bait jars containing chopped squid and herring. In each bay 50 pots were soaked for 24 hours and the five bays were fished on five consecutive days. The escape rings of the pots were sealed in order to retain smaller crabs and the mesh was 2-inch diamond-mesh. Approximately half of the pots were set between 0-9 meters and half were set between 10-25 meters (Figure 2). The location, set and retrieval times, and depth were recorded for each pot. The same pot

locations were used each sampling period using a military Global Positioning System (GPS) (Rockwell PLGR^{+}) with an accuracy of $\pm$ 3 m.

All species collected in the pots were counted and recorded. Dungeness crabs were examined further by sex, size, shell condition, appendage damage, and reproductive condition. Female Dungeness crabs were recorded as either ovigerous or nonovigerous. Carapace width (CW) was measured immediately anterior to the tenth anterolateral spine in millimeters with vernier calipers. Shell condition was determined by appearance and hardness: soft shells were soft to the touch; new shells had sharp spines, were bright in color, and were free of fouling organisms; old shells had dull spines, were not as bright in color, and had some fouling organisms; and very old shells had very dull spines and color, and had fouling organisms (Shirley and Shirley, 1988). Damage was recorded as missing, damaged, or regenerating for each appendage. Carapace damage was also recorded. Females were examined for matted setae, a condition in which the setae become blackened and matted after egg hatching. The condition of blackened pleopods is used as an indicator of recent female reproductive history because a female is assumed to have brooded eggs and not molted if she has blackened pleopods. The presence of sperm plugs and eggs were also recorded; the color of eggs was noted.

SCUBA Sampling

Dive transects were also used to sample crabs in each bay. Transects were 2 m x 100 m and were in the depth range of 0 (mean lower low water) to 18 m (Figure 2). Some transects were less than 100 m long because the depth limit was reached before the end of the transect. Transects were positioned systematically along the pot locations and

were placed perpendicular to the shore. Transects were further divided into quadrants 2 m x 10 m. Usually 20 dive transects were conducted in each bay during each sampling period. The number of males, females, and ovigerous crabs were recorded.

Tagging Study

A tagging study was added to the project in fall 1995. All crabs caught in crab pots and ovigerous females encountered by divers in South Beardslee Islands and Berg Bay (Figure 1) were tagged with 3" double-T Floy tags. The tags were positioned on the right posterior epimeral line near the branchial chamber. Each tag had data identifying the project and a unique number. 1,739 females were tagged: 1,427 were nonovigerous and 312 were ovigerous.

Statistical Analysis

Contingency tables, specifically G-tests, were used to test for independence in the proportion of nonovigerous and ovigerous females encountered in commercial crab pots, two depth strata, and dive transects for spring and fall samples. If the null hypotheses were rejected then the frequency of nonovigerous and ovigerous females caught were assumed to not be independent of season. When comparing the proportions of nonovigerous and ovigerous females caught with respect to season, fall 1998 data were not included since there were no spring 1998 data with which to pair. G-tests were also used to determine if the frequency of encountering male and female crabs was independent of season for both pot and dive data.

Paired t-tests were used for the pot data to examine if there were significant differences between ovigerous and nonovigerous carapace widths (CW) within spring

and fall samples. Ovigerous, nonovigerous and nonovigerous females with blackened pleopods were categorized into 8 size classes based upon CW which were each 10 mm except for the first size class which included all crabs smaller than 120 mm CW and the last size class which represented all females larger than 181 mm CW. A 2-way contingency table was used to test for significant differences between the proportion of ovigerous and nonovigerous females in each size class.

For pot data, G-tests were used to examine if the frequency of a female having one or more appendages damaged, missing or regenerating was independent of female reproductive status. Data were examined by season.

Potential effects of season and female reproductive state on carapace condition were tested using G-tests. Ovigerous females in soft-shell condition were not caught, therefore, the soft-shell condition was not included in the analyses.

Information collected from tagged and recaptured female crabs was used to extrapolate reproductive activity for individual crabs. Data, such as reproductive state at the time of tagging and recapture, whether the female molted, and whether she had blackened pleopods, were used as indicators of reproductive history. If a female had not molted between captures and did not have blackened pleopods it was assumed that she did not carry an egg clutch the previous reproductive period. Likewise, if a nonovigerous female was caught in the spring it was assumed that she did not reproduce that spring. If a female molted between when she was tagged and recovered, it was not possible to derive her recent reproductive history. All interpretation was based upon the assumption that blackened pleopods persist for approximately one year.

Statistics were calculated using StatView (1996) and by methods described in Sokal and Rohlf (1995). Values were considered significant when $P<0.05$ and highly significant when $P<0.01$.

Results

Data on 27,506 crabs were used in this study. Crab pot sampling accounted for 8,508 nonovigerous females, 476 ovigerous females and 14,537 males. On dive transects, 1,199 nonovigerous females, 1,240 ovigerous females and 1,546 males were encountered. These catches may not represent true population percentages of males, nonovigerous and ovigerous females due to different catchability rates. For example, crab pot sampling is biased against ovigerous females (O'Clair *et al.*, 1990). The size range for nonovigerous females caught in crab pots was 100 mm-190 mm carapace width (CW). Ovigerous females caught in crab pots ranged from 106 mm-180 mm CW and ovigerous females encountered on dive transects ranged from 114 mm-167 mm CW.

Seasonal Variations in Catch Rates

More nonovigerous than ovigerous females were caught in crab pots in both seasons (G-tests; Spring $G=110.5$, $P<0.0001$; Fall $G=13.0$ $P=0.04$, Figure 3a). Proportionally, more nonovigerous females were caught in crab pots during the fall samples than spring samples (G-test, $G=458.3$, $P<0.0001$, Figure 3b), and more ovigerous crabs were caught in pots during the spring samples than in the fall samples (G-test, $G=22.0$, $P=0.0005$, Figure 3b). These results suggest that more females are ovigerous in the spring, which is what is expected based upon current knowledge of Dungeness reproductive biology in southeastern Alaska.

Divers encountered more ovigerous females in the spring samples, and more nonovigerous females in the fall samples (G-test, Spring, G=51.0, P<0.0001; Fall, G=58.3, P<0.0001, Figure 4a). Nonovigerous females were encountered more often in the fall samples than spring; ovigerous females were encountered more often in the spring samples than fall (G-test, nonovigerous, G=30.8, P<0.001; ovigerous, G=126.7, P<0.0001, Figure 5b). Similar to the crab pot data, dive data support the current understanding of Dungeness crab reproduction in Alaska with more ovigerous females found in the spring samples.

More males than females were caught in crab pots for both the spring and fall samples (G-test, Spring, G=288.6, P<0.0001; Fall, G=556.1, P<0.0001, Figure 5a) which may have been the result of pot biases. Conversely, more females were encountered on dive transects than males for both sampling periods (G-test, Spring, G=87.0, P<0.0001; Fall G=36.8, P<0.0001, Figure 5b). Dive transect sampling is usually considered an unbiased sampling method, however different depth distributions for the sexes may account for bias in the dive data, which was restricted to depths less than 18 m.

Depth Distribution of Females

More nonovigerous females were found in shallow depth during the spring and at deeper depth in the fall (G-test, G=88.1, P<0.0001). However, no differences in the depth distribution among ovigerous females were detected between seasons. Within both the fall and spring samples, no differences were detected between the depth distribution of nonovigerous and ovigerous females.

Carapace Width and Occurrence of Blackened Pleopods

The carapace width of nonovigerous females (μ= 149.3 $\pm$ 0.3) from crab pots was highly significantly larger than that of ovigerous females (μ = 145.4 $\pm$ 0.7) in the spring samples (t-test, t=-5.5, P<0.0001, Figure 6). A significant difference in carapace width (CW) was not detected between nonovigerous females (μ = 150.2 $\pm$ 0.1) and ovigerous (μ = 148.6 $\pm$ 1.5) in the fall samples.

Distribution of females among 8 size classes was not independent of female reproductive status and proportionally more nonovigerous crabs were caught for every size class greater than 141 mm CW than ovigerous (G-test, G=56.0, P<0.0001, Figure 7). The highest proportion of nonovigerous females was between 151-160 mm (Figure 7). The highest proportion of ovigerous females was in the size class of 141-150 mm CW (Figure 7). Nonovigerous females with blackened pleopods were most frequent in the three size classes between 141-170 mm CW. The remaining 4 size classes had small proportions of blackened pleopods (Figure 7, Figure 8). The smallest female caught with blackened pleopods was 123 mm CW. All but three females with blackened pleopods were observed in the fall samples.

Appendage Injury

In the spring samples, a higher proportion of ovigerous females had one or more damaged appendages; in the fall samples, more nonovigerous females had damaged appendages (G-test, Spring, G=23.6 P<0.0001; Fall, G=4.3, P=0.04, Figure 9a). More nonovigerous females with one or more appendages damaged were caught in the fall samples, but most ovigerous females with one or more appendages damaged were caught

in the spring samples (G-test, nonovigerous, G=40.5, P<0.0001; ovigerous, G= 7.2, P<0.0001, Figure 9b). In contrast, the frequency of females with one or more appendages missing or regenerating was independent of female reproductive status and season.

Shell Condition

Among spring samples, proportionally more nonovigerous than ovigerous females were new shelled (45% vs. 6%) and proportionally more ovigerous than nonovigerous females were encountered that were old (86% vs. 54%) and very old shelled (8% vs. 1%) (G-test, G=308.4, p<0.0001; Figure 10a). In the spring samples, the largest proportions of nonovigerous females were old shelled (54%) followed by new shelled (45%). Soft and very old shelled nonovigerous females (1%) constituted a very small proportion of females caught in spring samples. Catches of ovigerous females in the spring were dominated by old shelled (86%) crabs followed by a small catch of new (6%) and very old shelled (8%) crabs and no soft shelled ovigerous females were caught (Figure 10a).

In the fall samples, proportionally more nonovigerous than ovigerous females were soft (7% vs. 0%) and very old shelled (21% vs. 10%) and proportionally more ovigerous females were caught that were new (31% vs. 26%) and old shelled (60% vs. 45%) (G-test, G=7.4, P=0.02, Figure 10b). In the fall samples, both nonovigerous and ovigerous females were most frequently caught as old shelled followed by new shelled, very old shelled and soft-shelled (Figure 10b). Ovigerous females that were new shelled in the fall may have molted, mated, hardened and extruded eggs whereas old shelled ovigerous females in the fall probably relied on stored sperm.

Proportionally more nonovigerous females were caught in the fall samples than spring samples that were soft (7% vs. 0%) and very old shelled (21% vs. 1%) and more new (45% vs. 26%) and old shelled (54% vs. 45%) nonovigerous females were caught in the spring samples (G-test, G=1136.8, P<0.0001, Figure 11a). The majority of nonovigerous females in the spring samples were old (54%) and new shelled (45%) and small percentages were soft (0%) and very old-shelled (1%) (Figure 11a). In the fall samples, the highest percentages of nonovigerous females were also old shelled (45%) and new shelled (26%) followed by smaller percentages of very old (21%) and soft shelled (7%) (Figure 11a).

Among the ovigerous females sampled, proportionally more new (86% vs. 60%) and very old shelled (10% vs. 8%) crabs were caught in the fall samples and more old shelled (86% vs. 60%) ovigerous females were caught in the spring samples (G-test, G=29.1, P<0.0001, Figure 11b). Within spring samples, old-shelled ovigerous females were the highest frequency encountered (86%) followed by very old-shelled (8%) and lastly, new-shelled (6%) ovigerous females (Figure 11b). The highest frequency of ovigerous crabs in the fall samples were also old shelled (60%) followed by new shelled (31%) and very old shelled (10%) (Figure 11b).

Mark and Recapture

Tag and recapture data of females can provide valuable information on the periodicity of egg extrusion (Table 1). In total 16 tagged females were recaptured. Of these, 8 had not extruded eggs annually, at least four did not reproduce for 2 years and at least two females skipped a year or more and then extruded eggs. Three females molted

between tagging and recapture; reproductive activity could not be determined for these crabs. All three crabs that molted increased in carapace width by 15 mm, which is probably the result of one molt. One female was recaptured after 5 months and the other two were recapture after 1 year (Table 1). In fall samples, three crabs were tagged while in a nonovigerous condition from the crab pot survey and a week later were recaptured by divers and had extruded eggs (Table 1).

Discussion

Crab pot and dive data support laboratory observations that females do not reproduce annually in Alaska. If all mature females were reproducing annually, there should be no or few nonovigerous females in the spring samples; however, thousands of nonovigerous females were caught in pots during the spring samples and hundreds of nonovigerous females were encountered during spring samples on dive transects (Figure 3a, Figure 4a). In addition, many tagged females were observed to skip a year or more of reproduction (Table 1). Factors such as size, presence of blackened pleopods, frequency of damaged, missing or regenerating limbs, and carapace condition were all examined in this study to compare how non-reproducing females differed from reproducing females.

Sampling Biases

Pot sampling has been considered a biased sampling method of female crabs, as pots underestimate the ovigerous population and perhaps the female population as a whole. The differences in capture rates may be due to different behavior activities of males, nonovigerous and ovigerous females. Ovigerous female Dungeness crabs in Alaska have been found to have reduced feeding behavior and foraging responses

(Schultz and Shirley, 1997), and are thus not as attracted to pots as nonovigerous females and males. An in situ ultrasonic tagging study of Dungeness crabs in Alaska found that ovigerous females were less active, move slower and utilized fewer habitats than male or nonovigerous crabs (O'Clair *et al.*, 1990). Conflicting results were obtained by a tagging study of Dungeness crabs in British Columbia. In the BC study, females tended to move about more than males (Smith and Jamieson, 1990). An important difference in these two studies was in the later study nonovigerous and ovigerous females were not examined separately and only two males and three female crabs were tagged. Ovigerous *Cancer pagurus* are also less active, may not feed and are not caught in crab pots as often as nonovigerous females (Naylor *et al.*, 1997). Ovigerous Dungeness crabs in Alaska also form dense aggregations (O'Clair *et al.*, 1990; O'Clair *et al.*, 1996). If a crab pot is not set close to an aggregation, the chance of collecting ovigerous females is reduced.

In theory, the dive transect data should not be biased since crabs do not have to move or respond to food to be sampled. However, due to diver limitations, transects were not sampled as deep as the crab pots were set. Dive transects may be laid upon ovigerous aggregations, but in this study, transects were laid with a systematic sampling design that should not present bias. Proportionally fewer ovigerous females were captured in crab pots than encountered on dive transects (Figure 3a, Figure 4a) and in the crab pot samples, more nonovigerous females were always caught than ovigerous females (Figure 3a). The possible pot bias was also illustrated when the proportions of males and nonovigerous and ovigerous females combined were examined for pot and dive data. More males were caught in crab pots for both the spring and fall samples (Figure 5a).

Alternately, more females were encountered on dive transects for both seasons (Figure 5b). This pot bias is in agreement with the laboratory studies of Schultz and Shirley (1997).

Size Comparisons of Non-reproducing and Reproducing Females

In the spring, ovigerous females were smaller than nonovigerous females. Ovigerous females from the fall samples were not significantly different in size than nonovigerous females (Figure 6). An explanation for the smaller size of ovigerous females in the spring and no significant difference in the fall was: larger crabs may have extruded eggs first and thus had already extruded eggs in the fall sample period. The ovigerous females collected in the fall may represent females that relied on stored sperm and did not mate, thus extruding eggs earlier than the females that molted, mated and hardened before extruding eggs. Molting among Dungeness crabs was thought to occur frequently during early life and yearly as maturity approached and skip molting was considered rare (MacKay, 1934). More recent research in California suggested that molting probabilities for small adult female Dungeness crab, $\leq$ 140 mm $\pm$ 5 mm CW (dependent upon the particular study) is close to one and drops to near zero for females larger than 155 mm $\pm$ 5 mm CW (Hankin *et al.*, 1989; Mohr and Hankin, 1989; Wainwright and Armstrong, 1993; Hankin and Xue, 1996). Therefore, larger females probably do not molt yearly and may rely more on stored sperm. By the time the spring samples were collected, all of the smaller females that molted and mated were ovigerous, thereby decreasing the mean carapace width size. Likewise, since larger females do not molt as frequently, they may be more likely to be nonovigerous; hence in the spring

samples the nonovigerous females are larger than the ovigerous females (Figure 6). Alternately, others have observed smaller adult Dungeness crab females molting and mating earlier in the molting season (Hankin *et al.*, 1997), but these females cannot extrude eggs until their carapace hardens.

Size dependent egg extrusion has been observed in other species. Larger female *Sesarma* sp. crabs were found brooding eggs throughout the reproductive season and smaller crabs were found carrying eggs only in the last part of the season (Zimmerman and Felder, 1991). In another study, the largest spiny lobsters mated or extruded eggs, the smallest lobsters molted and the intermediate sized lobsters either mated, or molted and mated (Lipcius and Herrnkind, 1987).

To examine carapace width in more detail, females were categorized into 8 size classes. Proportionally, more nonovigerous females were caught that were 141 mm CW and greater and proportionally, more ovigerous females were caught in the smaller size classes (Figure 7). This data suggests that females 140 mm CW and smaller reproduce more frequently than larger females. Proportionally more nonovigerous females may have been observed in the larger size classes because of the reduced molting probability of larger females. Large females probably rely on stored sperm, and extrude eggs less frequently than smaller females. Even with the reduced molting probability of larger females, large percentages of females over 151 mm CW were ovigerous. The modal size of nonovigerous females was between 151-160 mm CW and the modal size of ovigerous females was slightly smaller at 141-150 mm CW (Figure 7). A small number of nonovigerous females were collected at both extremes of the size class distribution. Few

females between 171-180 mm CW were ovigerous and no ovigerous females over 181 mm CW were observed. Five nonovigerous females over 181 mm CW were collected. Females appear to be able to extrude eggs by either utilizing stored sperm or by molting and mating until they reach approximately 181 mm CW. Furthermore, Hankin *et al.* (1997) suggest that all female Dungeness crabs appear to mate regardless of size if they molt. Smaller crabs were observed in the Hankin *et al.* study than were observed in this study.

Female Dungeness crabs are believed to be able to extrude eggs at approximately 90-100 mm CW (MacKay and Weymouth, 1935; Cleaver, 1949; Butler, 1960; Orensanz and Gallucci, 1988, O'Clair *et al.*, 1996). This study provided further data on the size of maturity of female Dungeness crabs in Alaska. Females as small as 106 mm CW were collected in the ovigerous state.

Occurrence and Size Distribution of Females with Blackened Pleopods

The condition of blackened pleopods is used as an indicator of recent female reproductive history. The setae of female crabs becomes matted or blackened after eggs have hatched. A female is assumed to have brooded eggs and not molted if she has blackened pleopods. However, all females may not produce blackened pleopods after egg hatching and before molting. In a recent study, females hatched eggs in the laboratory, but did not produce blackened pleopods (Swiney, 1999). The laboratory crabs were held in a sediment-free, clean environment that may have prevented the pleopods from blackening. Cleaning of pleopods has been suggested for *Cancer gracilis*

(Orensanz *et al.*, 1995), and occurs in laboratory reared Dungeness crabs (T. Shirley, unpublished observations).

The distribution of nonovigerous females with blackened pleopods was examined by size classes in this study. The majority of females with blackened pleopods were between 151-160 mm CW, but females with blackened pleopods were found in each size class except less than 120 mm CW (Figure 8). Essentially all of the females with blackened pleopods were collected in the fall samples, which suggests that these females brooded eggs in the previous spring and had not yet molted.

Numerous studies examining molting dynamics of female Dungeness crabs found that molting probability decreases rapidly after 135 mm CW (Hankin *et al.*, 1989). Examination of blackened pleopod data from this study support the hypothesis of reduced molting probability after 135 mm CW by an increase in blackened pleopods found in larger size classes (Figure 8). Although, the percentage of females with blackened pleopods began to decrease after 160 mm CW. The decrease in the percentage of females with blackened pleopods among females larger than 160 mm CW and the fact that essentially all of the females with blackened pleopods were collected in the fall suggest that blackened pleopods may persist for approximately one year. If blackened pleopods occur after egg hatching and until molting, it would be expected that the occurrence of blackened pleopods would continue to increase as size increased due to reduced molting probability for larger females, but this was not observed in this study. Furthermore, if blackened pleopods persist until a female molts, then females should be collected with blackened pleopods in the spring and fall samples, not just in the fall. Of all of the

nonovigerous females collected, only a small proportion had blackened pleopods (Figure 7). If blackened pleopods persisted until molting, then much larger percentages of nonovigerous females should have blackened pleopods, especially in the larger size classes. Females over 160 mm CW probably do not extrude eggs as frequently. The occurrence of blackened pleopods may be reduced, especially if blackened pleopods only persist for approximately one year and these females are skipping more than one reproductive season. Females observed with blackened pleopods probably brooded eggs the previous spring.

Comparison of Shell Condition between Non-reproducing and Reproducing Females

In the spring, 86% of ovigerous females sampled were old shelled (Figure 10a, Figure 11b). These females most likely molted, mated and extruded eggs the previous fall and by the time the spring samples were taken they were classified as old shelled. The largest proportion of nonovigerous females caught in the spring, which was a little over half, were also old shelled (Figure 10a, Figure 11b). This group may have molted at the same time as old shelled ovigerous females, but did not extrude eggs the spring they were sampled.

More new shelled crabs were nonovigerous that ovigerous in the spring (Figure 10a). These females may have molted in the winter and were therefore new shelled in the spring. If they did molt in the winter they would have missed the reproductive season. Proportionally, more ovigerous females were very old shelled than nonovigerous females (Figure 10a). Very old-shelled ovigerous females most likely relied on stored sperm to fertilize egg clutches. Soft-shelled ovigerous females were never caught because the

female must harden before egg extrusion (Figure 9a). Nonovigerous females that were soft shelled in the spring molted after the reproductive season.

The fall sample period is at the beginning of when females are expected to extrude eggs. A comparison of percentages of nonovigerous and ovigerous females during the fall sample will suggest which shell condition females extrude eggs first. In fall samples, the majority of ovigerous females caught were old shelled and proportionally more old shelled females were ovigerous than nonovigerous (Figure 10b, Figure 11b). These ovigerous females probably recently extruded eggs and since they were old shelled relied on stored sperm. Proportionally more new shelled crabs caught in the spring were also ovigerous, although the percentages were very close (Figure 10b).

Patterns of egg extrusion by shell condition can be derived by examining the different proportions of ovigerous females caught in the spring and fall samples. Old shelled females are caught proportionally more frequently in the spring and fall in comparison to the other shell conditions (Figure 11b). Females are beginning to extrude eggs during the fall sampling period, therefore ovigerous females in the fall are probably the first egg extruders. Sixty percent of the ovigerous females caught in the spring were old shelled and 31% were new shelled. These two shell conditions combined may constitute the 86% of old shelled ovigerous females seen in the spring samples. Females that were new shelled in the fall samples were probably classified as old shelled in the spring samples. The proportions of very old shelled ovigerous females sampled in the spring and fall were approximately the same (Figure 11b); suggesting that very old females only extrude eggs early in the reproductive season. The ovigerous females that

were very old in both spring and fall either used stored sperm to fertilize their egg clutches, or less likely, mated in a hard shell condition.

Occurrence of Appendage Injury in Nonovigerous and Ovigerous Females

A comparison of damaged, missing and regeneration of limbs was only significantly different between nonovigerous and ovigerous females for limbs damaged. Proportionally, more ovigerous females than nonovigerous females were found with at least one limb damaged in the spring samples. Alternately, more nonovigerous females were caught in the fall samples with one or more limbs damaged (Figure 9a). Among ovigerous crabs, more limbs were damaged in the spring samples than in the fall samples. This supports the hypothesis that damage among these crabs occurred during mating when the female was in a soft-shell state. Damage resulting from courting males and male-male agonistic encounters has been reported for blue crabs, *Callinectes sapidus* (Smith, 1992). The increase in ovigerous females with damaged limbs in the spring was probably not due to increased predation upon these females because one would expect them to have elevated levels of missing appendages, but they did not. Another study in southeastern Alaska found more appendage injuries occurred later in the year and may have been the result of molting, mating or commercial fishing (Shirley and Shirley, 1988). Missing or regeneration of limbs does not appear to restrict the ability of a crab to extrude eggs since the occurrence of crabs missing or regenerating limbs was independent of female reproductive state.

Depth Distribution of Nonovigerous and Ovigerous Females

Dungeness crabs are generally thought to move inshore during months of molting, mating and egg extrusion (MacKay, 1934; Diamond and Hankin, 1985). A study in British Columbia found no evidence of seasonal movements for Dungeness females (Smith and Jamieson, 1990). In the current study, proportionally more nonovigerous females were found in shallow depth during the spring and at deeper depth in the fall. The depth of ovigerous females was independent of season. Within both fall and spring seasons, there was no difference in the proportion of nonovigerous and ovigerous females caught in the two depth strata. Females that are relying on stored sperm may remain offshore (Diamond and Hankin, 1985). *Chionoecetes opilio* females that move to warmer water have a one year embryonic development cycle, whereas females that do not move to warmer water develop embryos on a two year cycle (Moriyasu and Lanteigne, 1998). Dungeness females in southeastern Alaska may have varying duration of embryonic development based upon movement to warmer or colder water. It should be noted that the fall surveys in this study occurred in September, which is believed to be near the beginning of the mating season. If females do move inshore for mating, they may not have moved before the September sampling. The crabs also may have been attracted to the crab pots and traveled from different depths.

Frequency of Reproduction as Derived from the Tagging Study

Females that were tagged and later recovered provided insight into individual female reproductive activity. On three separate occasions, females were caught in the crab pot sampling as nonovigerous and the following week were encountered on dive

transects as ovigerous crabs. This information provided further evidence that females are extruding eggs in the fall months in Alaska.

If using blackened pleopods is reliable as an indication of recent brooding of an egg clutch when a crab did not molt, considerable information on the reproductive activity of tagged crabs can be derived. It was assumed that blackened pleopods only persist for one year in the interpretation of data. In this study, eight females did not extrude eggs for at least one reproductive season and of these, half appear to not have reproduced for two seasons (Table 1). The tag data confirmed that at least two crabs did not reproduce one year and then reproduced the following year. These two individuals skipped at least one reproductive season, but were able to reproduce again in subsequent years and both were relatively large at 160 mm CW and 162 mm CW. These two females relied on stored sperm to fertilize their egg clutches since they did not molt between tagging and recapture (Table 1). Large females do not appear to stop extruding eggs, but can rely on stored sperm to fertilize an egg clutch, even after skipping at least one reproductive season.

Alternate Hypotheses for the Occurrence of Large Nonovigerous Females

Three hypotheses can explain why large nonovigerous females were found in the spring samples. Mature females may not reproduce annually. Gonadosomatic indexes were found to be significantly lower among females that extruded eggs when compared to females that did not extrude eggs. Furthermore, GSI and oocyte area of ovigerous females did not increase until after egg hatching (Swiney, 1999). Ovigerous females may not have the energy reserves to develop gonads until after egg hatching, due to the

reduced feeding and foraging behavior of ovigerous crabs (Schultz and Shirley, 1997). There may simply not be enough time for females to hatch eggs and then develop mature gonads, therefore females must skip at least one reproductive season.

An alternate explanation for relatively large numbers of nonovigerous females in the spring is that females may delay maturation. It may be beneficial for females to grow faster by not investing energy into reproduction and reach a size in which fecundity would be greater. This strategy may result in an increase in fitness, but there is no reason to suspect that female Dungeness crabs are delaying maturation.

Many females may have delayed reproduction because they were unable to find males to mate with and were therefore nonovigerous in the spring. A study in northern California examined this hypothesis. Hankin *et. al.* (1997) concluded that virtually all molting females regardless of size mated even though the exploitation rate of males in the system studied often exceeded 90%. The largest females that the Hankin *et. al.* (1997) study examined were approximately 166 mm CW. A small percentage of the females examined in this study were very large and may have been mate limited. It seems unlikely that the large percentages of nonovigerous female Dungeness crabs observed in this study delay reproduction due to a lack of males to mate with. In general, the reproductive success of a female is not limited by her ability to have her eggs fertilized, but by her ability to produce eggs (Trivers, 1972).

Parental Investment and Reproductive Strategies

Parental investments are usually associated with birds, primates and other vertebrates, but invertebrates can also invest energy into "parenting." Trivers (1972)

defines parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of survival (and reproductive success) at the cost of the parent's ability to invest in other offspring." Parental investment includes metabolic investment in primary sex cells as well as feeding or guarding of young (Trivers, 1972). Using this definition, it appears as if female Dungeness crabs put energy into parental investment. Results of this study and a previous study (Swiney, 1999) suggest that females are not reproducing annually, but rather invest in one brood at the expense of another. Ovigerous females have reduced feeding behavior (Schultz and Shirley, 1997) which may be a form of parental investment. A female can protect her brood by not actively foraging and making herself vulnerable to predators, at the expense of the next brood. If the female was eating while brooding eggs, then she may be able to develop mature gonads and extrude eggs every season, but instead starves herself to benefit the current brood. The size of parental investment is reflected in its negative affect on a parent's ability to invest in other offspring (Trivers, 1972). Parental investment among female Dungeness crabs is relatively high since it may preclude the development of a brood the following year.

Male Dungeness crabs also contribute to parental investment by guarding the female before and after she molts. These pre- and post mating embraces can last for up to two weeks (Snow and Neilsen, 1966). Crabs are very vulnerable when they are soft shelled. A male can assist in assuring his reproductive success by guarding a female when she is most vulnerable instead of mating with numerous females.

Organisms use a variety of reproductive strategies to ensure their reproductive success. In this study, it has been suggested that larger females extrude eggs first and do not reproduce annually and smaller females reproduce annually and extrude eggs later in the season. It may not seem intuitively advantageous for larger females to extrude eggs earlier since egg hatching appears to be synchronous and brooding eggs has a high cost to females since they have greatly reduced feeding behavior. Furthermore, egg parasites have more time to feed on eggs with increased brooding time. Despite the personal cost to the female, it may be beneficial for reproductive success of the female to extrude eggs earlier. Trivers (1985) suggested that "In general, the older parent the less will be its future reproductive success and the lower will be the cost of current investment, measured in terms of future offspring. This should select for a longer period of parental investment." This concept is observed in female Dungeness crabs in Alaska. Older females are brooding eggs longer and may thus be increasing their overall reproductive output by introducing larvae with higher survival potential.

Conclusions

Female crabs do not appear to reproduce annually in Alaska. Large numbers of nonovigerous females were caught in spring samples, a time in which females are ovigerous. In the spring samples, ovigerous females were smaller than nonovigerous females. Female Dungeness crabs have reduced molting probabilities after 135 mm CW (Hankin *et al.*, 1989). Larger females probably do not molt yearly and may rely on stored sperm to fertilize eggs. Nonovigerous and ovigerous females were observed over all size ranges except no ovigerous females over 180 mm carapace width were observed. Hankin

et al. (1997) observed smaller ovigerous females ranging from 116 to 166 mm CW in northern California. The largest proportion of females with blackened pleopods in the current study was between 141-170 mm CW. This group may be the largest contributor to the portion of the population that does not reproduce annually. These are larger females that are not molting annually and may either rely on stored sperm to fertilize egg clutches or may wait until they molt and mate next before extruding eggs. Examination of carapace condition found the two largest groups of nonovigerous females were new and old shelled. Proportionally more ovigerous females had one or more damaged limbs than nonovigerous crabs. The damage may have been the result of mating activity, because once eggs have been extruded ovigerous females are more sedentary (O'Clair *et al.*, 1996; Schultz and Shirley, 1997). Missing and regeneration of appendages does not appear to negatively affect egg extrusion. Tagged and recovered crabs demonstrate that some females can skip at least one mating season and extrude eggs at a later time without molting. Large females probably do not mate annually due to reduced molting probabilities, but they can rely on stored sperm to fertilize eggs.

Modified Reproductive Cycle

Data from this and a separate laboratory study (Swiney, 1999) can be applied to enhance the current knowledge of Dungeness crab reproductive cycles in Alaska (Figure 12). Dungeness crabs in Alaska were thought to begin mating and extrude eggs from September through November and the eggs hatch from April through August with the majority of hatching occurring in May and June (Shirley *et al.*, 1987). My data supports this general reproductive cycle. From the tagging portion of this study it appears as if

females are extruding eggs in September (Table 1) which is approximately when Shirley *et al.* (1997) suggested egg extrusion occurs. Likewise, in a laboratory study the eggs of all females hatched at the end of May (Swiney, 1999), which is approximately when Shirley *et al.* (1997) suggested hatching occurs.

Two different reproductive pathways may be followed by Dungeness crabs in Alaska based in part on crab size (Figure 12). Larger females tend to not molt and mate annually, but rather rely on stored sperm and skip reproductive seasons. Smaller females tend to molt, mate and extrude eggs annually. Egg extrusion may occur approximately August through January (Figure 12). Egg extrusion does not appear to be synchronous, but egg hatching appears to be relatively synchronous in southeastern Alaska (Swiney, 1999).

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Figures

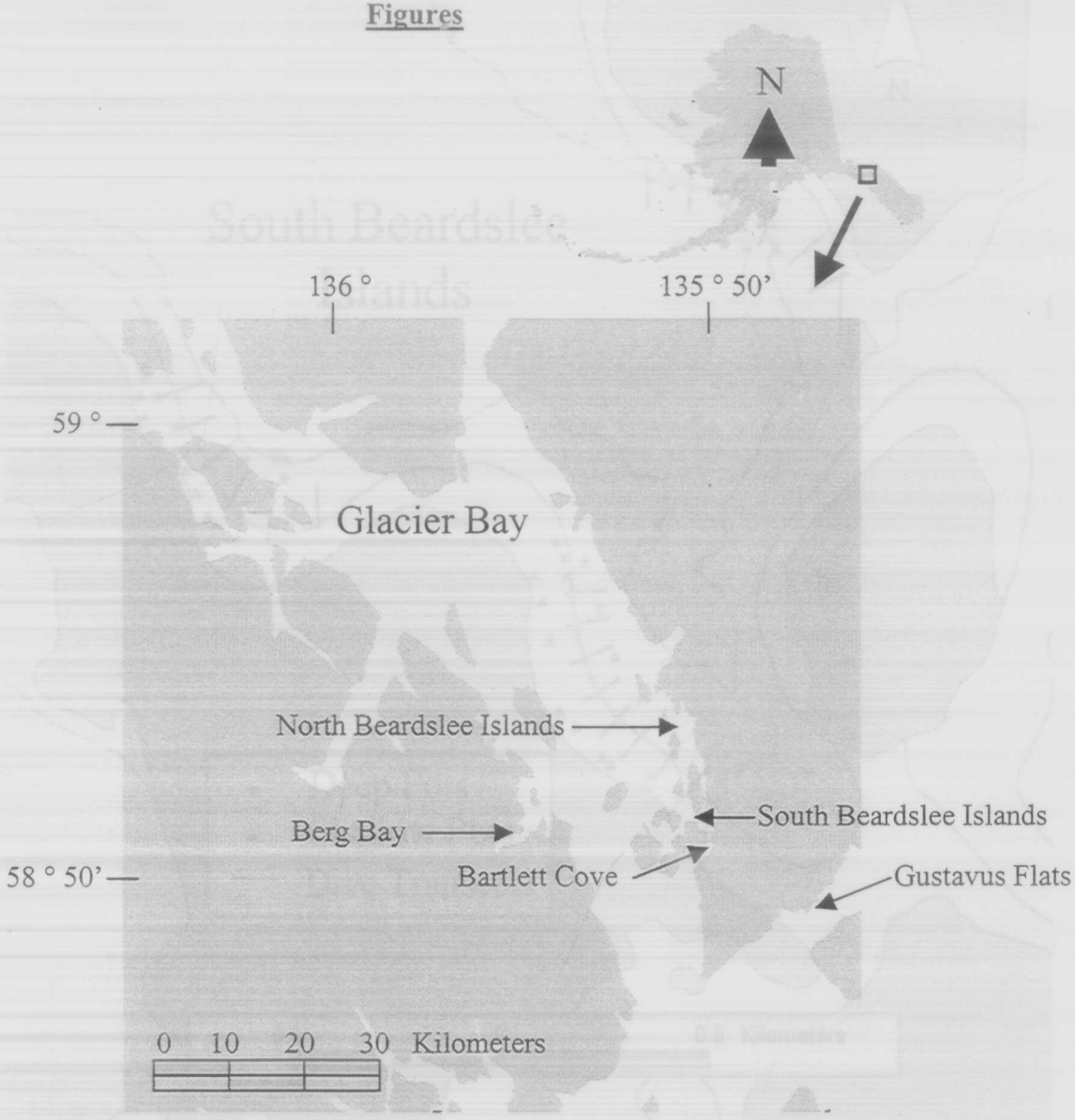

Figure 1. Study sites for crab pot and dive transect sampling. Sampling was conduced in April and September from 1992 through 1998.

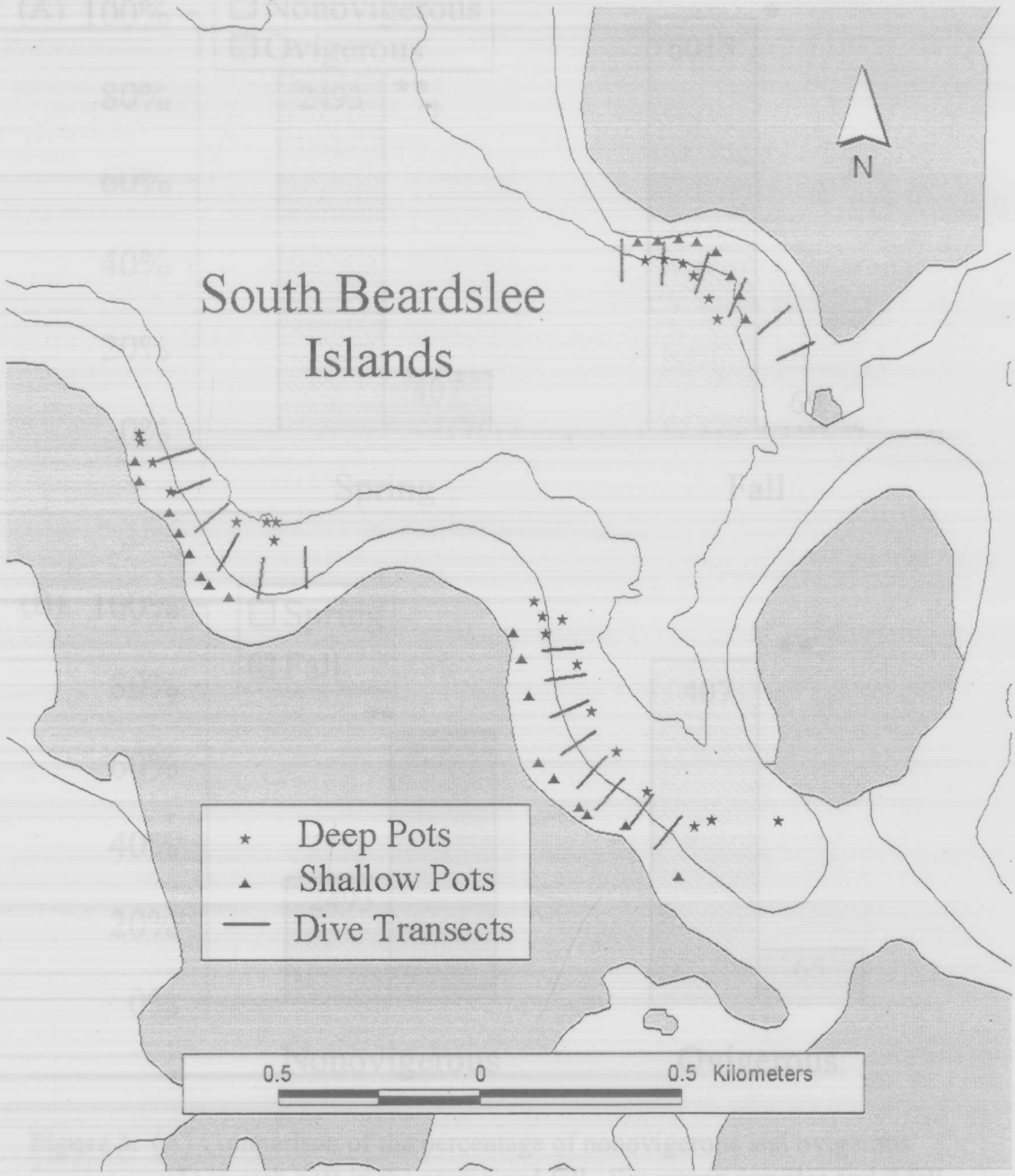

Figure 2. An example of crab pot and diver transect placement within study areas. Location of sampling efforts in South Beardslee Islands. Commercial crab pots were set in two depth strata. Shallow sets were 0-9 meters and deep sets were 10-25 meters. Dive transects were 2 meters x 100 meters and extended from 0-18 meters depth.

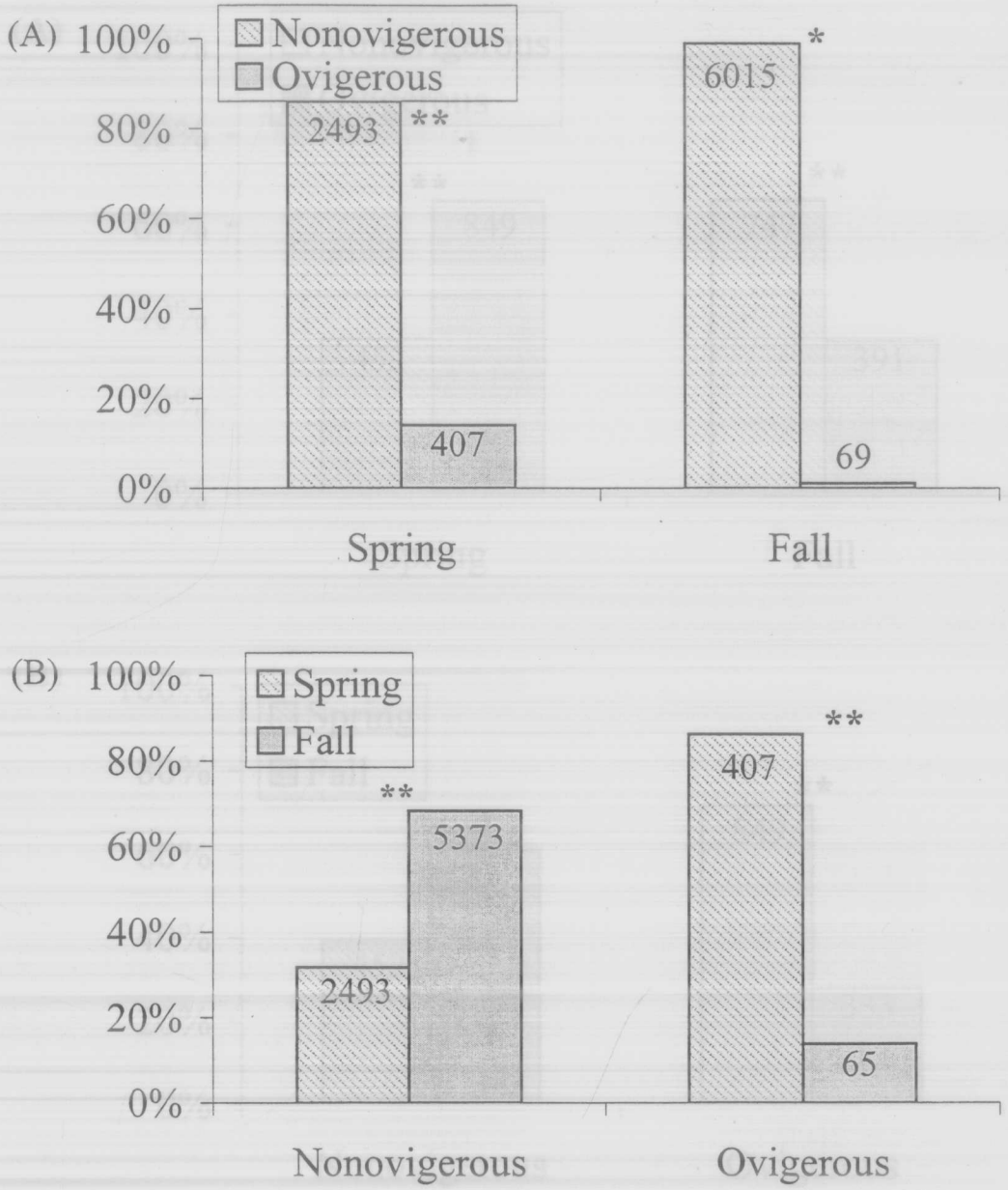

Figure 3. (A) Comparison of the percentage of nonovigerous and ovigerous females caught in crab pots in the spring and fall. Six spring samples and 7 fall samples are represented. (B) Comparison of the percentage of females caught in spring and fall samples from pots for nonovigerous and ovigerous females. Six spring and 6 fall samples are represented. Values in bars are numbers of crabs collected. * denotes significant difference and ** denotes highly significant differences

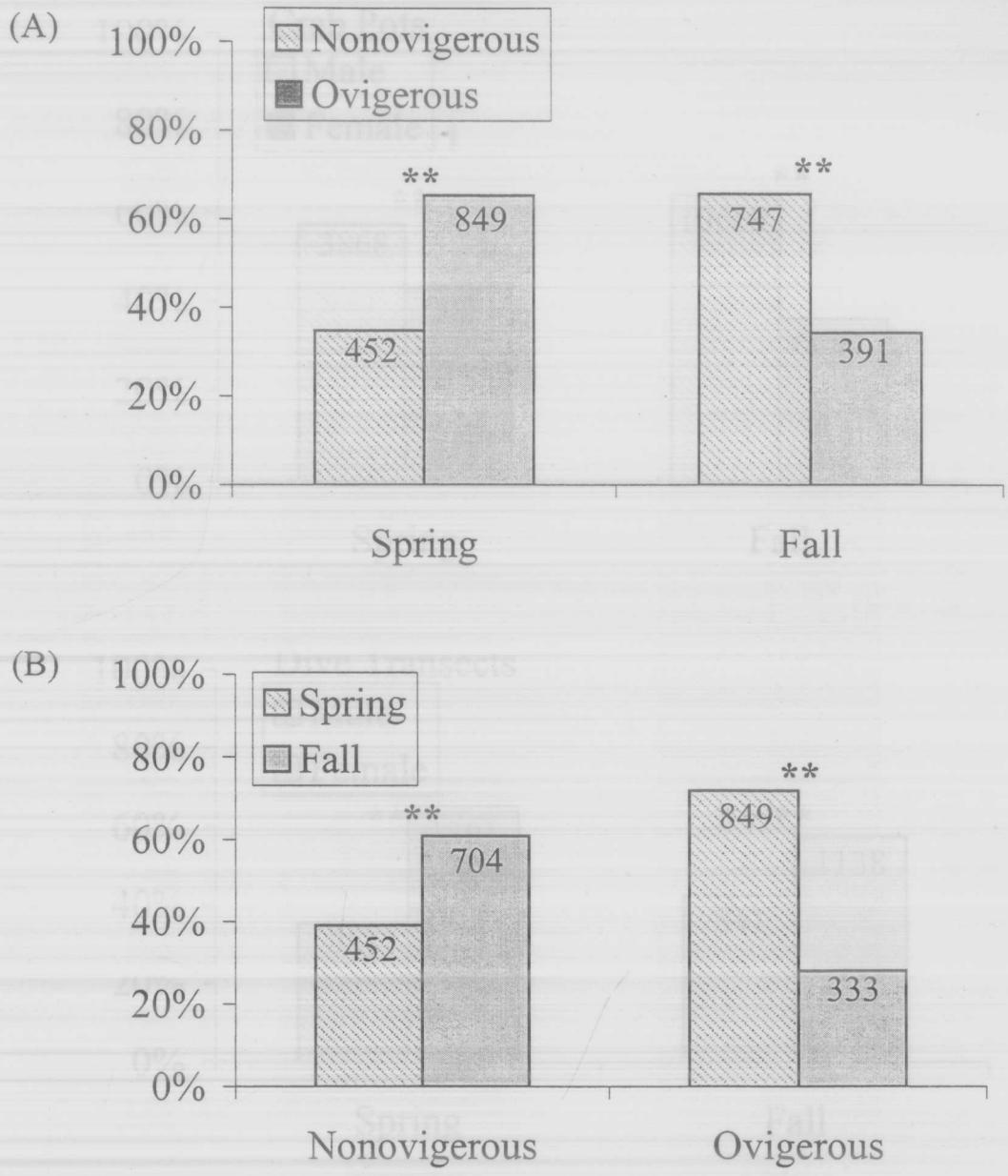

Figure 4. (A) Comparison of the percentage of ovigerous and nonovigerous females from SCUBA transects in the spring and fall. Six spring samples and 7 fall samples are represented. (B) Comparison of the percentage of females caught in spring and fall samples from SCUBA transects for nonovigerous and ovigerous females. Six spring and 6 fall samples are represented. Values in bars are numbers of crabs collected. ** denotes highly significant differences

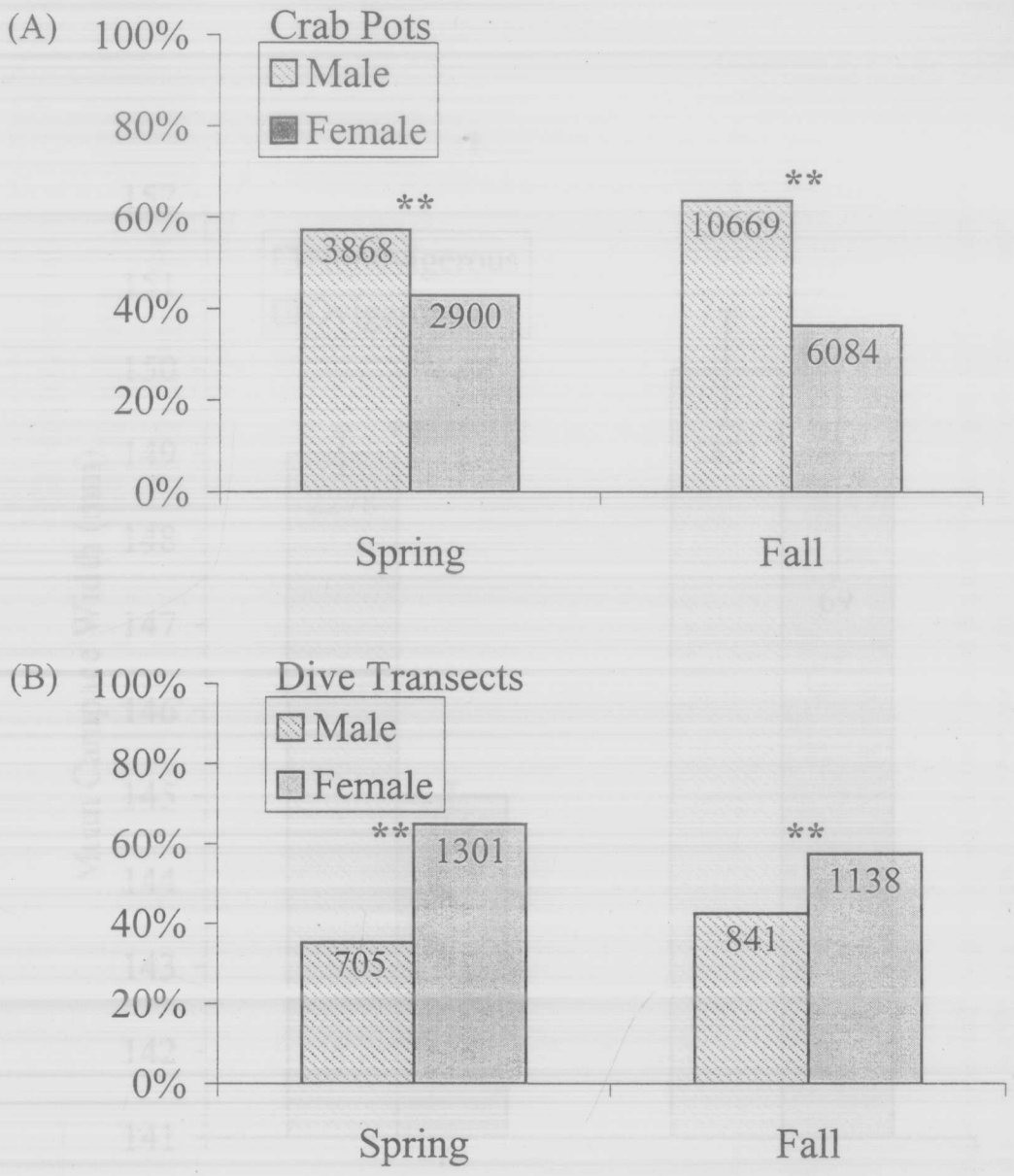

Figure 5. (A) Comparison of the percentage of males and females caught in crab pots by season. (B) Comparison of the percentage of males and females encountered on dive transects by season. Six spring and 7 fall samples are represented. Values in bars are numbers of crabs collected. ** denotes highly significant differences

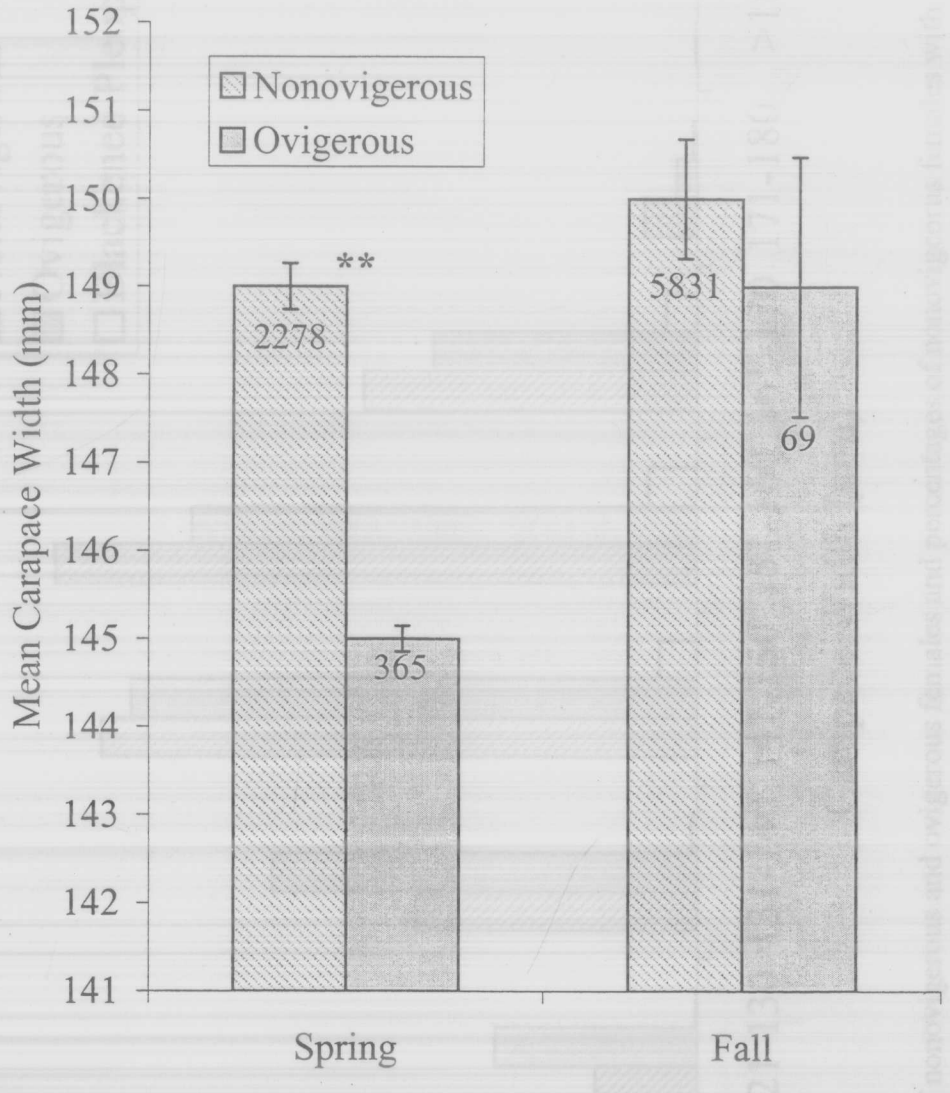

Figure 6. Mean carapace widths (CW) of ovigerous and nonovigerous females with respect to season. Values are mean ± one standard error (SE). ** denotes a highly significant difference between mean carapace width of nonovigerous and ovigerous females in the spring. No significant differences were detected for the fall.

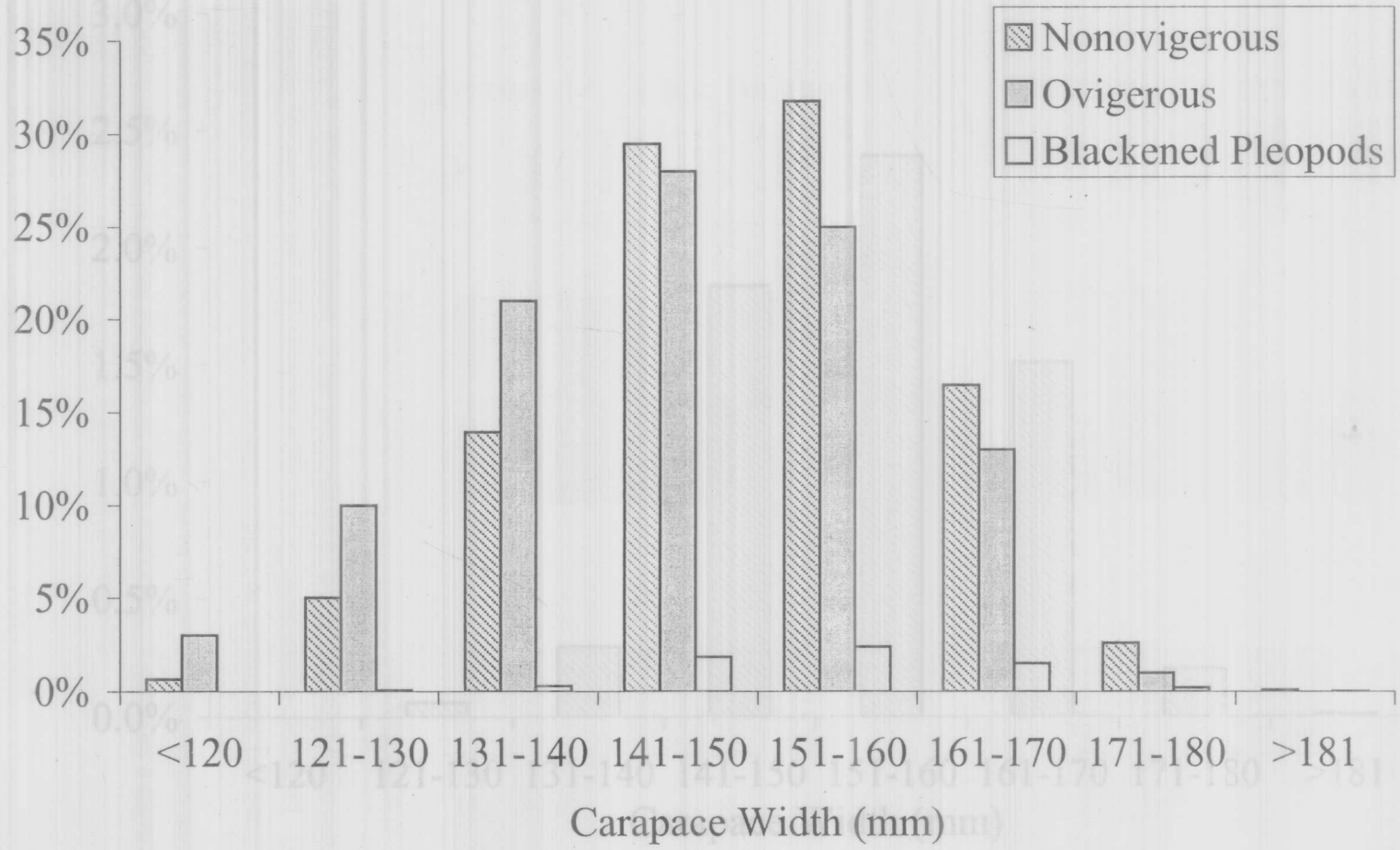

Figure 7. Distrubution of nonovigerous and ovigerous females and percentages of nonovigeorus females with blackened pleopods in10 mm carapace width size classes. 8500 nonovigerous, 434 ovigerous females, and 535 nonovigerous with blackened pleopods were collected.

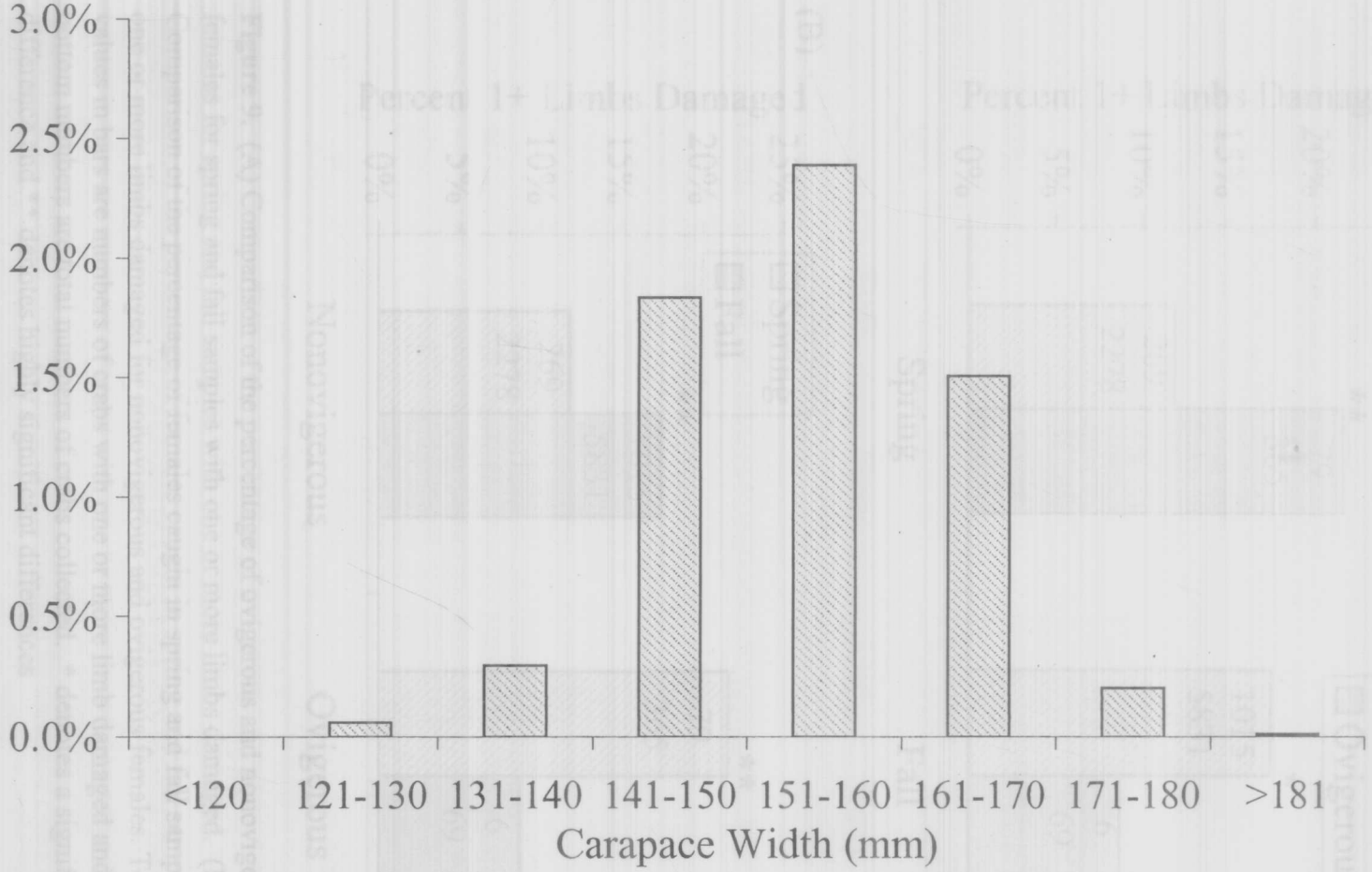

Figure 8. Percentage of females with blackened pleopods in 10 mm carapace width size increments. Sample size is 535.

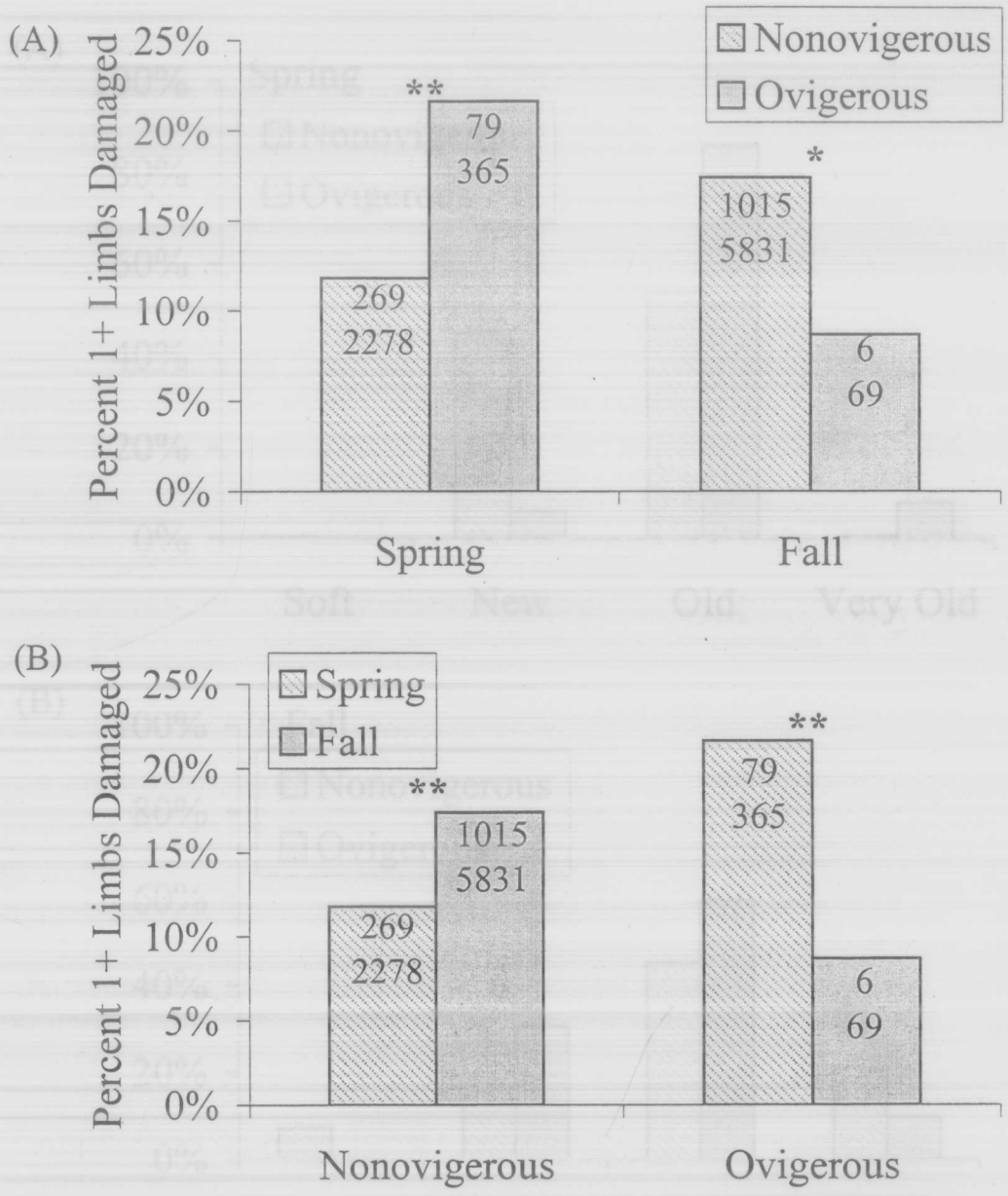

Figure 9. (A) Comparison of the percentage of ovigerous and nonovigerous females for spring and fall samples with one or more limbs damaged. (B) Comparison of the percentage of females caught in spring and fall samples with one or more limbs damaged for nonovigerous and ovigerous females. Top values in bars are numbers of crabs with one or more limb damaged and the bottom numbers are total numbers of crabs collected. * denotes a significant difference and ** denotes highly significant differences

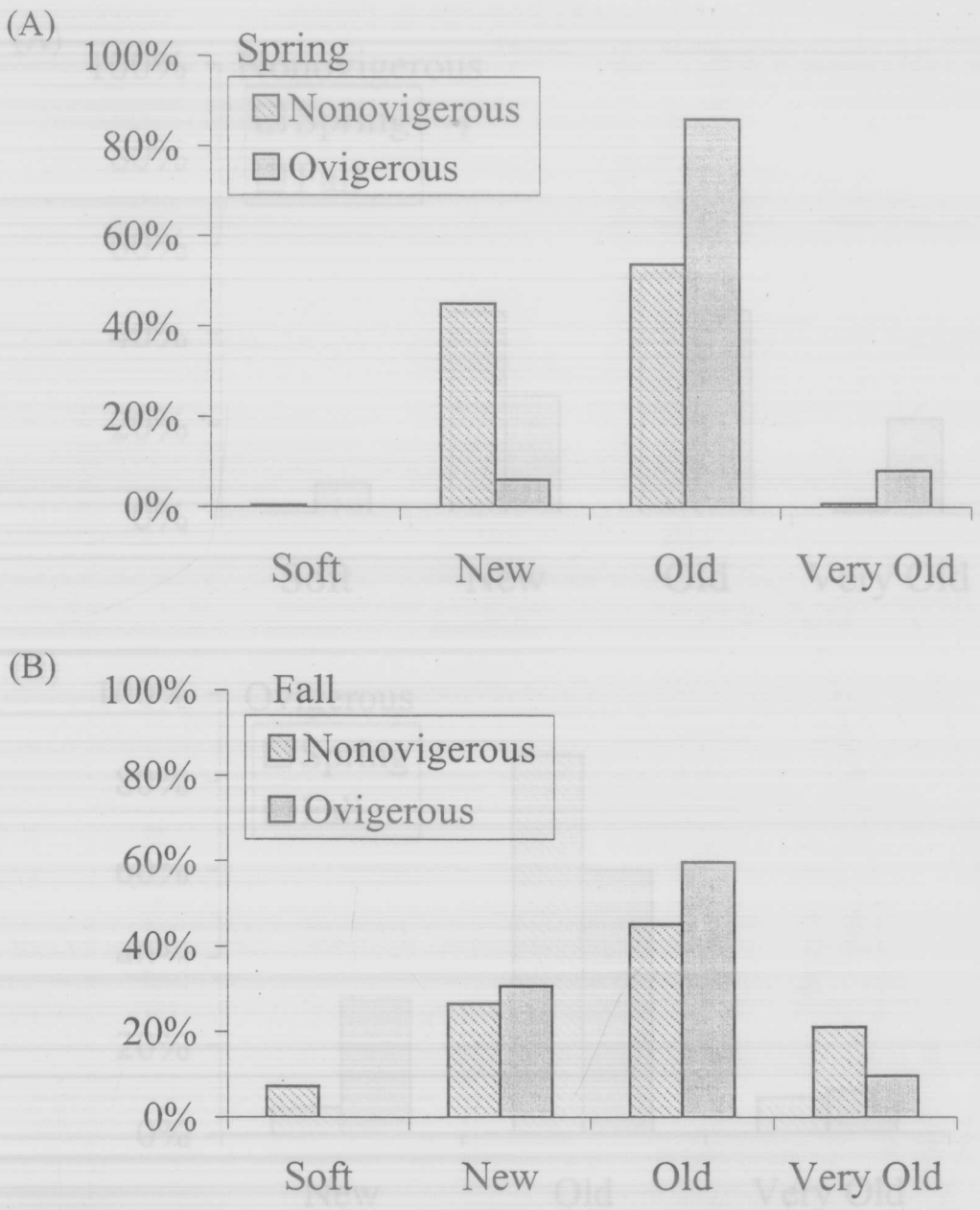

Figure 10. (A) Percentage of ovigerous and nonovigerous females from spring samples categorized by carapace condition. 2486 nonovigerous and 397 ovigerous females were collected. (B) Percentage of ovigerous and nonovigerous females from fall samples categorized by carapace condition. 6000 nonovigerous and 62 ovigerous females were collected.

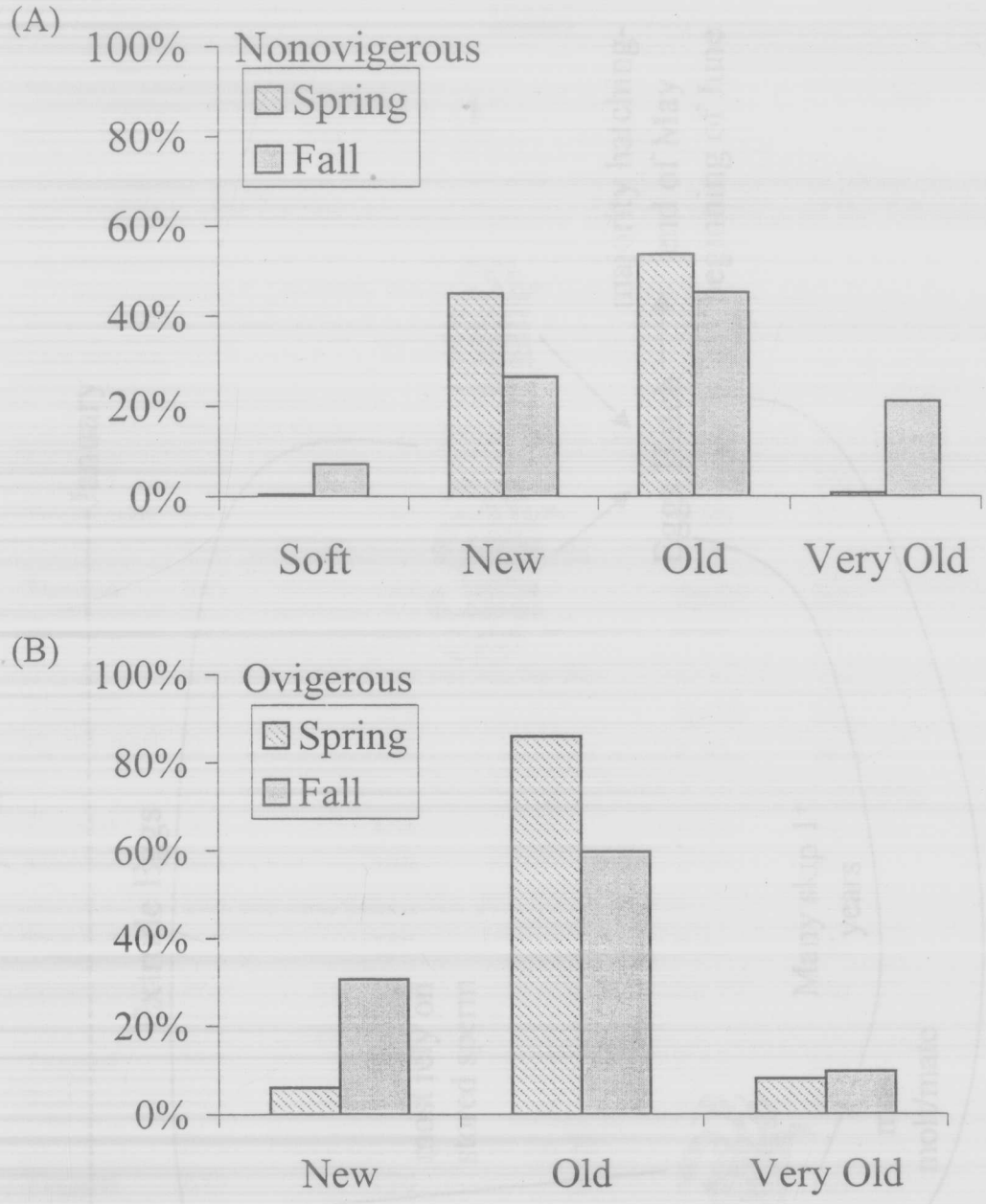

Figure 11. (A) Percentage of nonovigerous females categorized by carapace condition by season. 2486 nonovigerous females were collected in the spring and 6000 in the fall. (B) Percentage of ovigerous females categorized by carapace condition by season. 397 ovigerous were collected in the spring and 62 in the fall.

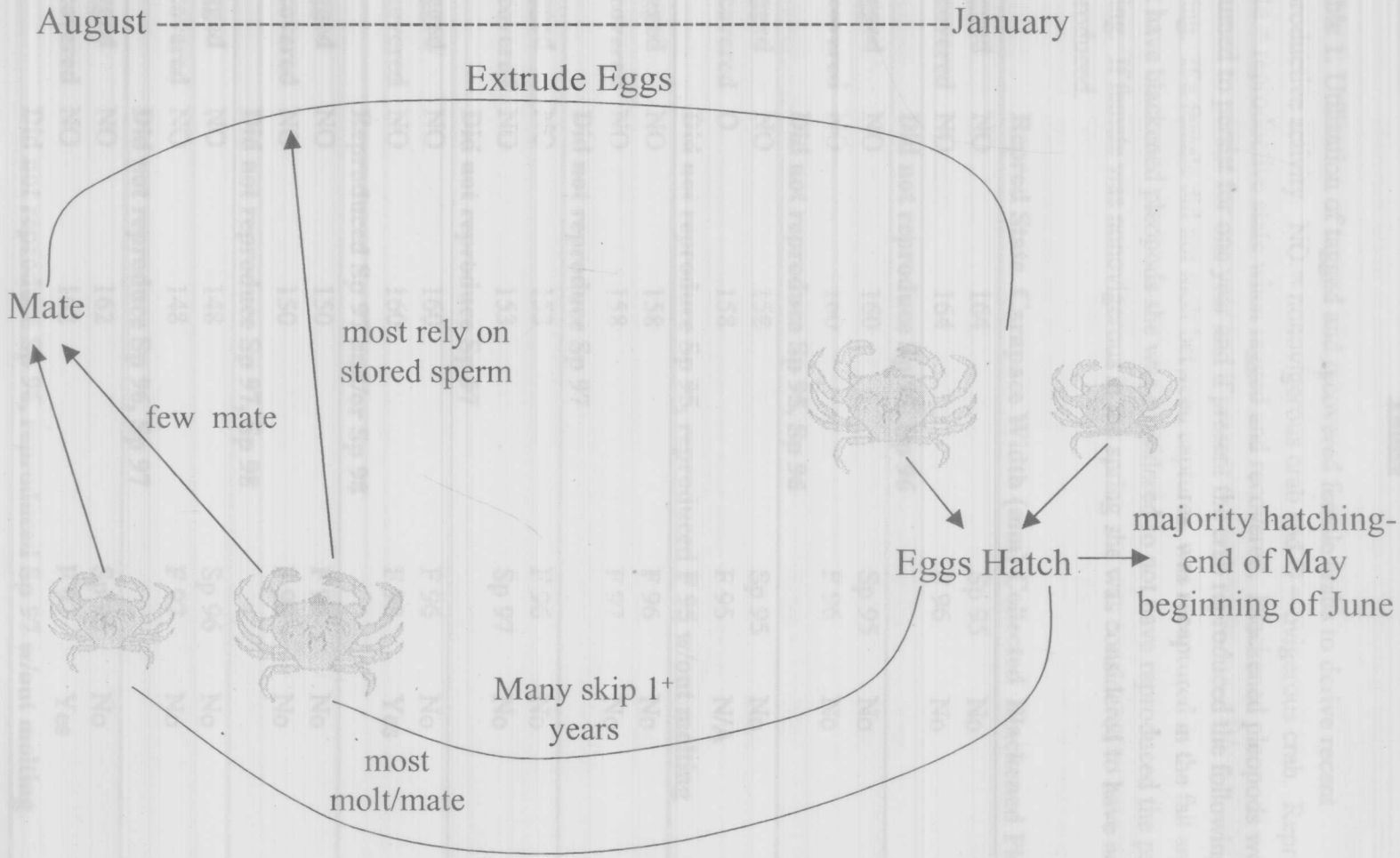

Figure 12. Suggested reproductive cycle of Dungeness crabs in southeastern Alaska. The smaller crabs represent females ≤ 140 mm carapace width and the larger crabs represent females >140 mm carapace width.

Tables

Table 1. Utilization of tagged and recovered female crabs to derive recent reproductive activity. NO = nonovigerous crab and O = ovigerous crab. Reprod state = reproductive state when tagged and recovered. Blackened pleopods were assumed to persist for one year and if present the crab reproduced the following spring. If a female did not molt between captures, was recaptured in the fall and did not have blackened pleopods she was considered to not have reproduced the previous spring. If female was nonovigerous in the spring she was considered to have not reproduced.

	Reprod State	Carapace Width (mm)	Collected	Blackened Pleopods
Tagged	NO	164	Sp 95	No
Recovered	NO	164	F 96	No
	Did not reproduce Sp 95, Sp 96			
Tagged	NO	160	Sp 95	No
Recovered	NO	160	F 96	No
	Did not reproduce Sp 95, Sp 96			
Tagged	NO	158	Sp 95	No
Recovered	O	158	F 95	N/A
	Did not reproduce Sp 95, reproduced F 95 w/out molting			
Tagged	NO	158	F 96	No
Recovered	NO	158	F 97	No
	Did not reproduce Sp 97			
Tagged	NO	153	F 96	No
Recovered	NO	153	Sp 97	No
	Did not reproduce Sp 97			
Tagged	NO	160	F 96	No
Recovered	NO	160	F 98	Yes
	Reproduced Sp 97 and/or Sp 98			
Tagged	NO	150	F 96	No
Recovered	NO	150	F 98	No
	Did not reproduce Sp 97, Sp 98			
Tagged	NO	148	Sp 96	No
Recovered	NO	148	F 97	No
	Did not reproduce Sp 96, Sp 97			
Tagged	NO	162	Sp 96	No
Recovered	NO	162	F 97	Yes
	Did not reproduce Sp 96, reproduced Sp 97 w/out molting			

Table 1 Contintued.

	Reprod State	Carapace Width (mm)	Collected	Blackened Pleopods
Tagged	NO	158	F 97	No
Recovered	NO	158	F 98	Yes
	Reproduced Sp 98			
Tagged	O	144	Sp 95	N/A
Recovered	O	159	F 96	N/A
	Reproduced Sp 95, F 96 molted			
Tagged	O	148	Sp 96	N/A
Recovered	NO	163	Sp 97	No
	Reproduced Sp 96 molted			
Tagged	NO	147	F 97	No
Recovered	NO	162	F 98	No
	Molted			
Tagged	NO	149	F 96	Yes
Recovered	O	149	F 96	N/A
	Reproduced Sp 96, extruded eggs between pot and dive sampling			
Tagged	NO	149	F 98	No
Recovered	O	149	F 98	N/A
	Extruded eggs between pot and dive sampling			
Tagged	NO	172	F 98	No
Recovered	O	172	F 98	N/A
	Extruded eggs between pot and dive sampling			

Appendices

Appendix 1. Date, method, location and number of Dungeness crabs collected. Crabs were collected by three methods: SCUBA divers, commercial crab pots, and wading at night of spring tides with flashlights and dip-nets. Ovigerous and nonovigerous females represent reproductive state at the time of collection and were not amended to denote females that extruded eggs in the immediate months following collection.

Date	Method	Location	Ovigerous	Nonovigerous	Male
09/15/97-		Glacier Bay			
09/19/97	Pots	National Park			100
10/14/97	Dip-net	Bridgett Cove			
10/15/97	Dip-net	Bridgett Cove		8	
10/16/97	Dip-net	Bridgett Cove		7	
10/17/97	Dip-net	Bridgett Cove		15	
10/18/97	Dip-net	Bridgett Cove		10	
10/19/97	Dip-net	Bridgett Cove		1	
10/25/97	SCUBA	Bridgett Cove		1	
11/01/97	SCUBA	Sheep Creek			
11/01/97	Dip-net	Bridgett Cove		18	
11/02/97	Dip-net	Bridgett Cove		26	
11/06/97	SCUBA	Bridgett Cove		15	
11/12/97	Dip-net	Bridgett Cove			
11/13/97	Dip-net	Bridgett Cove		1	
11/14/97	Dip-net	Bridgett Cove		6	
11/15/97	Dip-net	Bridgett Cove		5	
11/16/97	Dip-net	Bridgett Cove		14	
11/17/97	Dip-net	Bridgett Cove		3	
03/10/98	SCUBA	Bridgett Cove	25	18	
04/25/98	Dip-net	Bridgett Cove	30		
06/12/98	Dip-net	Bridgett Cove			
06/13/98	Dip-net	Bridgett Cove			
06/22/98	Dip-net	Bridgett Cove	1		
06/24/98	Dip-net	Bridgett Cove			
06/28/98	Pots	Bridgett Cove			
06/30/98	Pots	Bridgett Cove			
07/5/98	Pots	Bridgett Cove		10	
07/16/98	Pots	Bridgett Cove			
07/31/98	Pots	Bridgett Cove			10
08/25/98	Pots	Bridgett Cove	3	9	
09/16/98	Pots	Bridgett Cove	2		11
10/3/98	Pots	Bridgett Cove	1	7	
10/5/98	Dip-net	Bridgett Cove		3	

Appendix 2. Weekly measurements of temperature and salinity in flow-through tanks where Dungeness crabs were reared in this study. Temperature measured in °C and salinity was measured parts per thousand with a refractometer.

Date	Temp	Salinity
11/02/97	7.5	30
11/10/97	7.3	30
11/18/97	7.2	32
11/25/97	6.6	31
12/01/97	5.7	30
12/08/97	4.3	31
12/16/97	6.2	31
12/22/97	6.2	31
12/29/97	4.7	32
01/06/98	6.1	33
01/12/98	5.6	32
01/21/98	5.8	32
01/28/98	5.9	31
02/05/98	5.2	33
02/10/98	5.4	32
02/17/98	5.4	32
02/24/98	4.8	32
03/03/98	5.2	31
03/10/98	4.8	32
03/17/98	4.7	32
03/24/98	4.6	31
03/31/98	4.8	31
04/07/98	5.2	31
04/14/98	5.4	31
04/21/98	5.4	31
04/28/98	5.7	31
05/05/98	5.9	30
05/12/98	5.5	32
05/18/98	5.8	32
05/27/98	6.3	32
06/09/98	6.9	32
06/16/98	7.7	31
06/22/98	7.6	30
06/30/98	8.1	30
07/08/98	8.2	30
07/17/98	8.2	30
07/21/98	8.6	30
07/28/98	9.2	30

Appendix 2. Continued

Date	Temp	Salinity
08/04/98	8.2	30
08/11/98	9.6	30
08/21/98	9.0	31
08/25/98	8.8	30
09/01/98	9.0	30
09/08/98	8.9	30
09/15/98	9.1	30
09/29/98	9.3	30
10/07/98	9.0	31
10/14/98	8.6	31
10/20/98	9.0	30
10/27/98	7.9	30

Appendix 3. Month, carapace width (CW) mm, sex/reproductive condition, gonadosomatic index, and mean oocyte area mm for all Dungeness crabs dissected in this study. Sex/reproductive condition 1 = laboratory male, 2 = laboratory female that did not reproduce in 1997, 3 = laboratory female that reproduced in 1997, 4 = male from field, 5 = nonovigerous female from the field, 6 = ovigerous female from the field, 7 = laboratory female that did not reproduce in 1997 and extruded eggs in 1998, and 8 = laboratory female that extruded eggs in both 1997 and 1998.

Month	CW	Sex	GSI	Oocyte Area
MARCH	166	1	0.04%	
MARCH	173	1	0.06%	
MARCH	160	1	0.10%	
MARCH	155	1	0.15%	
MARCH	161	1	0.16%	
MARCH	181	1	0.16%	
MARCH	182	1	0.15%	
MARCH	184	1	0.17%	
MARCH	181	1	0.11%	
MARCH	165	1	0.18%	
MARCH	184	1	0.14%	
MARCH	189	1	0.19%	
MARCH	158	2	10.09%	0.131
MARCH	152	2	8.65%	0.082
MARCH	153	2	7.35%	0.091
MARCH	150	2	7.14%	0.084
MARCH	170	2	12.26%	0.1
MARCH	155	2	14.61%	0.109
MARCH	124	2	7.93%	0.1
MARCH	159	2	6.15%	0.07
MARCH	129	2	4.14%	0.047
MARCH	154	2	14.72%	0.092
MARCH	146	3	1.32%	0.009
MARCH	138	3	1.21%	0.006
MARCH	136	3	0.50%	0.005
MARCH	147	3	1.94%	0.007
MARCH	139	3	1.19%	0.005
MARCH	134	3	0.75%	0.003
MARCH	123	3	0.30%	0.003
MARCH	158	3	1.62%	0.006
MARCH	149	3	0.43%	0.005

Appendix 3. Continued

Month	CW	Sex	GSI	Oocyte Area
MARCH	152	3	0.64%	0.005
APRIL	154	1	0.22%	
APRIL	163	1	0.12%	
APRIL	161	1	0.25%	
APRIL	148	1	0.22%	
APRIL	156	1	0.17%	
APRIL	163	1	0.16%	
APRIL	177	1	0.19%	
APRIL	170	1	0.13%	
APRIL	166	1	0.16%	
APRIL	182	1	0.13%	
APRIL	158	2	8.26%	0.321
APRIL	133	2	9.88%	0.363
APRIL	158	2	4.88%	0.085
APRIL	148	2	14.42%	0.178
APRIL	159	2	10.03%	0.148
APRIL	159	2	11.62%	0.145
APRIL	146	2	4.79%	0.197
APRIL	166	5	12.10%	0.549
APRIL	155	5	15.00%	0.242
APRIL	153	5	15.72%	0.214
APRIL	147	3	2.04%	0.13
APRIL	137	3	2.07%	0.113
APRIL	124	3	0.36%	0.046
APRIL	134	3	0.73%	0.062
APRIL	144	3	0.96%	0.067
APRIL	123	6	0.73%	0.103
APRIL	160	6	1.27%	0.086
APRIL	155	6	0.68%	0.056
APRIL	137	6	0.77%	0.065
APRIL	144	6	1.30%	0.087
MAY	111	2	1.38%	0.064
MAY	107	2	1.71%	0.103
MAY	120	2	9.35%	0.288
MAY	155	2	17.03%	0.472
MAY	122	2	7.83%	0.346
MAY	106	2	9.25%	0.364
MAY	151	2	14.65%	0.441

Appendix 3. Continued

Month	CW	Sex	GSI	Oocyte Area
MAY	157	2	17.26%	0.53
MAY	119	2	7.69%	0.282
MAY	119	2	5.10%	0.243
MAY	147	3	1.20%	0.07
MAY	146	3	1.03%	0.082
MAY	119	3	0.66%	0.037
MAY	147	3	1.22%	0.061
MAY	166	3	2.20%	0.111
MAY	130	3	0.81%	0.055
MAY	147	3	0.75%	0.053
MAY	130	3	0.67%	0.043
MAY	146	3	2.41%	0.096
MAY	149	3	1.74%	0.091
MAY	178	1	0.21%	
MAY	152	1	0.19%	
MAY	157	1	0.11%	
MAY	156	1	0.16%	
MAY	158	1	0.21%	
MAY	152	1	0.14%	
MAY	155	1	0.27%	
MAY	183	1	0.13%	
MAY	148	1	0.05%	
MAY	159	1	0.12%	
JUNE	150	3	1.56%	0.081
JUNE	139	3	3.69%	0.129
JUNE	149	3	3.79%	0.152
JUNE	149	3	3.29%	0.146
JUNE	166	3	3.47%	0.151
JUNE	152	3	4.95%	0.206
JUNE	147	3	5.48%	0.247
JUNE	144	3	0.88%	0.054
JUNE	148	3	6.05%	0.244
JUNE	132	3	6.56%	0.238
JUNE	144	2	18.43%	0.587
JUNE	114	2	0.44%	0.046
JUNE	158	2	14.23%	0.509
JUNE	130	2	14.86%	0.607
JUNE	124	2	13.15%	0.456

Appendix 3. Continued

Month	CW	Sex	GSI	Oocyte Area
JUNE	147	2	15.73%	0.533
JUNE	155	2	19.34%	0.63
JUNE	122	2	1.34%	0.078
JUNE	153	2	17.42%	0.562
JUNE	130	2	15.35%	0.673
JUNE	157	1	0.10%	
JUNE	170	1	0.27%	
JUNE	173	1	0.12%	
JUNE	153	1	0.17%	
JUNE	188	1	0.17%	
JUNE	153	1	0.17%	
JUNE	174	1	0.18%	
JUNE	170	1	0.25%	
JUNE	166	1	0.10%	
JUNE	160	1	0.12%	
JULY	161	2	18.84%	0.809
JULY	146	2	17.20%	0.534
JULY	106	2	10.44%	0.458
JULY	155	2	20.20%	0.59
JULY	156	2	15.32%	0.544
JULY	146	2	18.35%	0.513
JULY	154	2	6.91%	0.287
JULY	159	2	17.20%	0.502
JULY	144	2	17.15%	0.651
JULY	149	2	15.38%	0.577
JULY	134	3	0.75%	0.055
JULY	149	3	10.22%	0.554
JULY	137	3	10.63%	0.705
JULY	137	3	0.92%	0.066
JULY	122	3	0.95%	0.048
JULY	156	1	0.26%	
JULY	152	1	0.39%	
JULY	149	1	0.22%	
JULY	162	1	0.16%	
JULY	154	1	0.18%	
JULY	156	1	0.12%	
JULY	158	1	0.17%	
JULY	158	1	0.12%	

Appendix 3. Continued

Month	CW	Sex	GSI	Oocyte Area
JULY	155	1	0.31%	
JULY	159	1	0.36%	
JULY	150	5	14.66%	0.449
JULY	142	5	10.99%	0.39
JULY	144	5	12.83%	0.439
JULY	159	5	2.31%	0.097
JULY	149	5	11.46%	0.434
JULY	138	5	1.12%	0.071
JULY	160	5	21.56%	0.512
JULY	139	5	0.90%	0.045
JULY	143	5	1.14%	0.075
JULY	148	5	3.46%	0.155
AUGUST	152	2	23.69%	0.698
AUGUST	124	2	17.42%	0.639
AUGUST	132	2	18.06%	0.616
AUGUST	157	2	18.50%	0.513
AUGUST	153	2	22.53%	0.64
AUGUST	133	2	18.82%	0.563
AUGUST	152	2	24.81%	0.599
AUGUST	143	2	15.77%	0.487
AUGUST	158	2	22.15%	0.619
AUGUST	158	2	21.91%	0.63
AUGUST	157	1	0.16%	
AUGUST	161	1	0.21%	
AUGUST	172	1	0.13%	
AUGUST	150	1	0.25%	
AUGUST	151	1	0.26%	
AUGUST	156	1	0.18%	
AUGUST	169	1	0.20%	
AUGUST	160	1	0.27%	
AUGUST	157	1	0.28%	
AUGUST	169	1	0.25%	
SEPTEMBER	131	3	15.10%	0.645
SEPTEMBER	149	3	10.05%	0.393
SEPTEMBER	163	1	0.30%	
SEPTEMBER	151	1	0.34%	
SEPTEMBER	182	1	0.23%	
SEPTEMBER	193	1	0.21%	

Appendix 3. Continued

Month	CW	Sex	GSI	Oocyte Area
SEPTEMBER	155	1	0.17%	
SEPTEMBER	197	1	0.08%	
SEPTEMBER	163	1	0.19%	
SEPTEMBER	162	1	0.16%	
SEPTEMBER	193	1	0.19%	
SEPTEMBER	153	1	0.13%	
SEPTEMBER	155	4	0.27%	
SEPTEMBER	160	4	0.18%	
SEPTEMBER	168	4	0.17%	
SEPTEMBER	168	4	0.15%	
SEPTEMBER	160	4	0.13%	
SEPTEMBER	151	4	0.14%	
SEPTEMBER	142	4	0.10%	
SEPTEMBER	147	4	0.11%	
SEPTEMBER	138	2	15.63%	0.645
SEPTEMBER	150	2	24.60%	0.616
SEPTEMBER	129	2	17.39%	0.557
SEPTEMBER	159	2	20.18%	0.664
SEPTEMBER	128	2	17.29%	0.639
SEPTEMBER	150	2	25.23%	0.641
SEPTEMBER	128	2	16.45%	0.473
SEPTEMBER	150	2	24.82%	0.596
SEPTEMBER	166	2	24.55%	0.702
SEPTEMBER	120	2	16.49%	0.581
SEPTEMBER	156	2	25.48%	1.111
SEPTEMBER	160	5	3.53%	0.159
SEPTEMBER	157	5	2.26%	0.076
SEPTEMBER	160	5	12.72%	0.367
SEPTEMBER	160	5	23.28%	0.752
SEPTEMBER	158	5	17.58%	0.608
SEPTEMBER	153	5	21.35%	0.601
SEPTEMBER	164	5	24.69%	0.646
SEPTEMBER	144	5	23.75%	0.713
SEPTEMBER	142	5	23.66%	0.699
SEPTEMBER	151	7	0.55%	
SEPTEMBER	152	7	0.67%	
SEPTEMBER	149	7	1.28%	
SEPTEMBER	128	7	0.43%	

Appendix 3. Continued

Month	CW	Sex	GSI	Oocyte Area
SEPTEMBER	151	7	1.15%	
SEPTEMBER	140	7	0.74%	
SEPTEMBER	161	7	0.92%	
SEPTEMBER	146	7	0.61%	
SEPTEMBER	149	7	1.58%	
SEPTEMBER	166	7	1.13%	
OCTOBER	179	1	0.22%	
OCTOBER	164	1	0.37%	
OCTOBER	198	1	0.09%	
OCTOBER	162	1	0.16%	
OCTOBER	146	1	0.17%	
OCTOBER	157	1	0.17%	
OCTOBER	173	1	0.25%	
OCTOBER	158	1	0.33%	
OCTOBER	180	1	0.21%	
OCTOBER	164	1	0.19%	
OCTOBER	159	4	0.11%	
OCTOBER	161	4	0.16%	
OCTOBER	166	4	0.22%	
OCTOBER	147	4	0.12%	
OCTOBER	179	4	0.11%	
OCTOBER	163	4	0.30%	
OCTOBER	166	4	0.12%	
OCTOBER	146	4	0.09%	
OCTOBER	148	4	0.11%	
OCTOBER	157	4	0.08%	
OCTOBER	162	6	0.83%	
OCTOBER	145	6	0.65%	
OCTOBER	149	6	1.77%	
OCTOBER	140	3	24.07%	
OCTOBER	149	3	24.66%	
OCTOBER	145	3	19.31%	0.778
OCTOBER	141	3	17.00%	0.392
OCTOBER	141	3	17.91%	0.685
OCTOBER	145	2	11.72%	0.486
OCTOBER	160	2	14.47%	1.048
OCTOBER	138	2	7.69%	0.529
OCTOBER	152	2	6.57%	1.386

Appendix 3. Continued

Month	CW	Sex	GSI	Oocyte Area
OCTOBER	121	2	14.27%	0.749
OCTOBER	124	2	13.42%	0.595
OCTOBER	151	2	16.85%	0.566
OCTOBER	148	2	10.91%	0.51
OCTOBER	156	2	13.68%	0.507
OCTOBER	150	2	5.48%	0.83
OCTOBER	162	5	4.32%	0.137
OCTOBER	162	5	2.59%	0.13
OCTOBER	153	5	9.00%	0.295
OCTOBER	159	5	17.65%	0.625
OCTOBER	152	5	8.18%	0.271
OCTOBER	144	5	7.46%	0.242
OCTOBER	150	5	18.68%	0.572
OCTOBER	159	5	1.03%	0.101
OCTOBER	122	5	11.67%	0.527
OCTOBER	156	5	7.04%	0.254
OCTOBER	146	7	0.91%	
OCTOBER	154	7	1.12%	
OCTOBER	129	7	0.72%	
OCTOBER	151	7	0.93%	
OCTOBER	154	7	1.08%	
OCTOBER	155	7	1.05%	
OCTOBER	154	7	0.86%	
OCTOBER	149	7	1.14%	
OCTOBER	140	7	0.77%	
OCTOBER	144	8	0.83%	
OCTOBER	145	8	0.68%	
OCTOBER	146	8	1.29%	

Appendix 4. Dates females extruded eggs in the laboratory. Crabs above line represent females that extruded eggs in 1997 and immediately after collection. Females below the line represent females that were reared in the laboratory and extruded eggs in 1998. * denote females that extruded eggs in 1997 and 1998.

Date	CW
11/19/97	137
11/19/97	156
11/11/97	152
11/14/97	154
11/14/97	146
11/21/97	158
11/25/97	148
12/01/97	134
12/01/97	145
12/01/97	134
12/02/97	149
1/22/98	137
1/22/98	137
1/22/98	146
1/22/98	147
8/19/98	149
8/23/98	129
8/27/98	146
8/27/98	166
8/27/98	152
9/03/98	149
9/03/98	154
9/03/98	161
9/09/98	154
9/10/98	149
9/10/98	146
9/14/98	151
9/18/98	146
9/19/98	154
9/19/98	128
9/21/98	140
9/23/98*	144
9/23/98	151
9/25/98*	146
9/28/98	140
9/28/98*	145
10/5/98	155